REPRODUCTIVE ECOLOGY AND POPULATION VIABILITY OF BREWER'S SPARRows AT THE NORTHERN EDGE OF THE BREEDING RANGE

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ABSTRACT

I examined the population dynamics of the provincially red-listed Brewer's Sparrow (Spizella breweri breweri) of British Columbia. This declining grassland bird reaches the northwestern limit of its breeding range in the province. My objectives were: 1) to explore spatial and temporal dynamics in fecundity and survival, 2) to model population viability based on these rates, 3) to examine the relative influences of vital rates on the population trend, and 4) to explore the relationship between the selection of nest site habitat characteristics and nest success.

I found that seasonal fecundity was highest when the nest predation rate was low, the number of clutches/female was high and when breeding began later in the season. High seasonal fecundity alternated between the sites. The best site in 1998 became the least productive in 1999 and vice-versa, and a third site was most productive in 2000. The over-riding factor driving spatial and temporal variation in productivity was shifting rates of nest predation. However, elevation-related storm effects when breeding began early, and variation in the number of clutches laid, were partly responsible for this variation. Adult female survival varied between years, from a high of 66% in 1997-1998, an El Niño year, to a low of 26% from 1998-1999, a La Niña year. Survival did not vary between sites.

A population viability model based on these demographic rates predicted that the population will decline to extinction within 100 years without immigration. For a best-case scenario where mean adult survival was high and years of low survival occurred every 10 years, population growth rate ($\lambda$) = 0.93. For a worst-case scenario where mean
adult survival was low and years of low survival occur at random, \( \lambda = 0.78 \). Sensitivity analysis showed that the population growth rate was most sensitive to adult survival.

Brewer's Sparrows selected nesting habitat that concealed nests. However, habitat variables related to concealment did not differ strongly between successful and depredated nests. Selected nest sites may not be the most successful because predation risk varies at larger spatial scales, and because the several generalist predators with differing search strategies cover all the possible safe havens.
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Chapter 1:

General Introduction

Current rates of biodiversity loss through human-caused extinction far exceed historical levels (Pimm et al. 1995, Pimm and Raven 2000). Birds are the taxon for which the most complete and reliable information is available. Some recent estimates suggest that 11% of the world’s bird species are endangered (Collar et al. 1994, May et al. 1995). It has been argued that the current, widespread decline in biodiversity requires conservation efforts to be focused at the ecosystem or landscape level (Franklin 1993). Combining a coarse-filter, landscape approach with fine scale species-level studies is crucial to the elucidation of the causal factors driving the extinctions that ultimately threaten ecosystem integrity (Simberloff 1988, Hunter 1991, James et al. 1996, Thomas and Martin 1996, Marzluff and Sallabanks 1998).

Concern about declining North American bird populations has generated a wealth of information on population trends and conservation status (e.g. Hagan and Johnston 1992, Finch and Strangel 1993, Martin and Finch 1995, Thomas and Martin 1996, Marzluff and Sallabanks 1998, Sauer et al. 2001). Although clear and persistent population declines have been observed in many species, the demographic mechanisms behind these declines remain unclear. Research priorities need to be focussed on (i) demographic characteristics of declining populations, (ii) environmental factors critical to demography and dispersal, (iii) the effects of human activities on demography and (iv) developing realistic population models for conservation planning and adaptive management (James et al. 1997, Derrickson et al. 1998). This approach allows us to establish the critical connections between changes in bird populations and habitat...
alteration at broad scales, particularly for groups of birds in severely altered habitats such as grasslands.

Population Declines of North American Grassland Birds

Populations of grassland-breeding birds have declined more steeply and across wider geographic areas than any other groups of North American birds (Vickery et al. 1999). Breeding Bird Survey (BBS) data indicate that 61% of grassland breeding species declined significantly from 1966-2000 (Sauer et al. 2001). Widespread and continuing habitat loss, degradation and fragmentation are thought to be responsible for these declines (Herkert 1994, Knopf 1994, Vickery et al. 2000). For example, since European colonization, tallgrass prairie habitat has been reduced by 82% in Manitoba and 99% in Iowa (Samson and Knopf 1994). Sixty percent of the original shrubsteppe habitat in Washington has been lost due to agricultural conversion (Dobler et al. 1996). Population declines are occurring in widespread species such as Western Meadowlark (*Sturnella neglecta*) and Horned Lark (*Eremophila alpestris*) as well as in those with more restricted ranges such as Baird’s (*Ammodramus bairdii*) and Henslow’s Sparrows (*A. henslowii*). Such general declines indicate serious threats to grassland ecosystems at the continental scale.

Despite these alarming patterns, few studies have examined the demographic characteristics of declining grassland bird populations throughout their lifecycles. Broad-based population changes can be due to a) poor reproduction, b) low adult and/or juvenile survival in non-breeding areas or c) mortality during migration. Productivity of grassland birds may be impaired through habitat alteration and fragmentation. Temple *et
al. (1999) found higher breeding productivity in grasslands without cattle grazing than in either continuously grazed or rotationally grazed sites. Suppression of the natural fire cycle may affect productivity negatively. Shriver and Vickery (2001) found that Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) nesting success increased when a more natural fire cycle was reintroduced. Fragmentation of prairie habitats and fire suppression led to increased nest predation and parasitism rates in five species of grassland birds in tallgrass prairie habitat (Johnson and Temple 1990). Vander Haegen *et al.* (2002) found higher nest predation rates in four passerine species in fragmented than in continuous shrubsteppe habitat. Thus, anthropogenically modified grassland habitats appear to be of poorer quality than more natural habitats for many grassland songbirds.

Most populations of North American grassland breeding birds are migratory, spending the part of the year in southern non-breeding areas, from the southern United States to parts of South America (Vickery *et al.* 1999). Similar forces to those on breeding grounds are causing alteration of habitats used by grassland birds during migration and winter, particularly increased urbanization and agriculture, including livestock grazing (Hutto 1986, Paige and Ritter 1999, Vickery *et al.* 1999). The non-breeding season ecology of most grassland birds is poorly understood and it remains unclear whether reduced survival due to habitat alteration on non-breeding grounds is a significant contributor to observed declines (Vickery *et al.* 1999). Recent work has described habitat associations of some wintering and migrating grassland birds. Henslow's Sparrow density during winter was higher in areas with more herbaceous plant cover and more recent timber harvest and/or fires (Plentovich *et al.* 1999). Igl and
Ballard (1999) found that 21 species of grassland birds occurred in higher densities in shrub-grassland habitats with < 30% woody cover, and occurred in wider variety of habitats than previously documented. In Arizona, winter densities of Vesper (Poecetes gramineus) and Savannah (Passerculus sandwichensis) Sparrows were higher and Cassin’s Sparrows (Aimophila cassinhi) were lower in areas of spring/summer burning and cattle grazing (Gordon 2000).

Work on habitat selection in winter is a useful first step; however, there is little direct evidence linking habitat selection or alteration to survival. In order to understand and ultimately reverse or slow the declines in grassland birds, it is crucial to determine whether events in breeding or non-breeding areas most affect population declines.

The Biology and Conservation Significance of Peripheral Populations

Several patterns of decline in bird populations have been identified, including range contractions, with and without reductions in core density, and reduced overall densities without changes to geographical ranges (Wilcove and Terborgh 1984, Thomas 1996). Whether peripheral populations are important to the conservation of a species in decline remains a source of debate in the conservation literature and may depend on the pattern of decline across the range (Hunter and Hutchinson 1994, Lesica and Allendorf 1995, Channel and Lomolino 2000, Rodriguez 2002). By examining the geographic pattern of decline for a species, we may gain insight into the causes of the decline and determine where best to focus conservation efforts.

Within the geographical range of many species, density tends to be highest in a few core areas and increasingly lower towards the range periphery (Brown 1984, Gaston
The size of peripheral populations may be more variable over time at range edges due to limiting resources and harsh environmental conditions (Curnutt et al. 1996, Shreeve et al. 1996). These qualities may make peripheral populations more prone to extinction through loss of genetic diversity, and demographic and environmental stochasticity (Maurer and Brown 1989, Lesica and Allendorf 1995, Curnutt et al. 1996, Garcia-Ramos and Kirkpatrick 1997). As species decline, small peripheral populations fluctuating in size may disappear resulting in a range contraction toward the core (Lawton 1995, Mehlman 1997, Newton 1997). For these reasons, the conservation value of peripheral populations may be low compared to more abundant, stable core populations.

Alternatively peripheral populations may be crucial to the conservation of a species. Peripheral populations may have high conservation value because their isolation can lead to divergence, contributing disproportionately to the genetic variation within the species (Hunter and Hutchinson 1994, Shreeve et al. 1996). Over the long-term, greater genetic diversity within a species facilitates adaptation to changing conditions. Populations in marginal, variable habitats may have evolved characteristics that allow them to respond to environmental extremes and periodic change, traits that may be crucial for species survival in a scenario of global climate change. Thus, the long-term protection of a species may depend on protecting peripheral, genetically distinct populations (Faith 1992, Lesica and Allendorf 1995).

Peripheral populations may also be important sites for the initiation of range shifts due to climate change. There is growing evidence that many species are expanding northward and to higher elevations in response to recent climate warming (Thomas et al.
These range expansions depend upon dispersal from current range boundaries, making peripheral sites important priorities for the maintenance of ecological and evolutionary processes that will determine future biodiversity. As well, healthy peripheral populations may provide immigrants to rescue core populations in decline. Breininger (1999) showed that in a declining population of Florida Scrub Jays, as core territories became vacant they were filled by immigrants from peripheral areas.

Recent evidence supports the idea that peripheral populations are critical for species conservation as it suggests that range contraction may not be the general pattern for declining species. Channell and Lomolino (2000) showed that 68% of 245 declining species from a diversity of taxa maintained a greater proportion of their historic range peripheries than their range cores. Ninety-one of those species remained only in the edges of their historical ranges while five (<1%) showed range contraction by remaining only in the range core. They suggest that declines were concentrated in core areas because habitat loss was greater there relative to the range edges. Similarly, Rodriguez (2002) demonstrated that most declines in 27 North American bird species (including four grassland species) were concentrated in the high-density core areas and not in the peripheral areas of the ranges. Although these two studies revealed similar patterns, the conclusions about where conservation efforts should be focussed were contradictory. Channell and Lomolino (2000) suggested that, if core populations continue to decline, peripheral populations will become increasingly important and should be protected. Rodriguez (2002) assumed that overall species declines were being driven by processes in core populations and therefore, this is where habitat needs to be protected to avoid
further losses. This ongoing debate would be greatly informed by research examining the demographic processes operating in core versus peripheral populations and relating those processes to observed patterns of decline.

Ecology of the Brewer’s Sparrow

The Brewer’s Sparrow is a small, open-cup nesting migratory songbird of western North America. There are currently two recognized subspecies, the sagebrush (*Spizella breweri breweri*) and the timberline (*S. b. taverneri*; Rotenberry *et al.* 1999). Differences in plumage, song, habitat and genetics lead some authors to consider them separate species (Sibley and Monroe 1990, Klicka *et al.* 1999; but see Mayr and Johnson 2001). The sagebrush (*breweri*) subspecies breeds at lower elevation, in semi-arid habitats throughout the Great Basin region from southern British Columbia, Alberta and Saskatchewan, to northern Arizona and New Mexico (Rotenberry *et al.* 1999). The timberline (*taverneri*) subspecies is known to breed in shrubby sub-alpine habitat in two widely separated mountainous areas: one group in south-western Alberta and south-eastern British Columbia and the second in north-western British Columbia, south-western Yukon and adjacent areas in Alaska (Rotenberry *et al.* 1999). The distribution of these two groups may not be this discrete. Breeding populations likely occur between these two regions, but remain unrecorded due to the remote location and rugged terrain (Rotenberry *et al.* 1999). Due to differences in elevation and breeding habitat, the two subspecies do not appear to overlap in breeding range. Brewer’s Sparrows winter in desert and sagebrush shrubland habitats from southern California, Arizona and New Mexico through central Mexico and Baja (Rotenberry *et al.* 1999). Information on the
ecology and distribution of the subspecies or breeding populations in non-breeding areas is scarce. I restricted my study to the \textit{breweri} subspecies and all further use of “Brewer’s Sparrow” in this thesis refers to \textit{breweri} only, unless otherwise noted.

Brewer's Sparrow breeding habitat is generally dominated by Big Sagebrush (\textit{Artemesia tridentata}), with an understory of mixed bunchgrasses and forbs (Wiens and Rotenberry 1981). Nests are placed close to the ground near the centre of live shrubs, usually Big Sagebrush (Rotenberry \textit{et al.} 1999). Average clutch size is 3 - 4 eggs and several broods may be attempted during the breeding season (Rotenberry \textit{et al.} 1999, Mahony \textit{et al.} 2001). Brewer's Sparrows have been described as being semi-colonial due to their habit of nesting in fairly dense congregations in patches of suitable habitat (Rotenberry \textit{et al.} 1999).

Like many grassland-breeding birds of North America, Brewer's Sparrows have shown a disturbing population decline. Breeding Bird Survey (BBS) data show a significant range-wide decline of 3% per year from 1966-2000 (Sauer \textit{et al.} 2001). However, this decline is not consistent across the breeding range. Populations in core areas of their distribution such as Idaho and Oregon have declined significantly (5.2% and 2.5% per year respectively), whereas peripheral populations in New Mexico and Washington appear stable (Sauer \textit{et al.} 2001). These declines are thought to be driven by widespread and continuing loss, fragmentation, and alteration of shrubsteppe breeding habitat (Rotenberry \textit{et al.} 1999, Paige and Ritter 1999).

In British Columbia, Brewer's Sparrow breeding is limited to the shrubsteppe ecosystem of the southern Okanagan and Similkameen valleys, an area approximately 2700 km$^2$ in size, from the USA border north to Penticton, and from Keremeos east to the
Okanagan River. This region is the northwestern limit of the breeding range and the northernmost extension of the Great Basin region (Rotenberry et al. 1999, Campbell et al. 2001). The population trend in British Columbia is unknown since BBS data are inadequate and no other long-term population trend data exist. Brewer's Sparrows are provincially red-listed (endangered) in British Columbia due to their limited breeding range and threatened shrubsteppe habitat (Government of B.C. 1997). This region has one of the highest levels of biodiversity in Canada and provides habitat for many species at risk (Mosquin et al. 1995). Warman (2001) found that in order to maintain current population levels of twenty-nine threatened vertebrate species, 37.2% of the region would have to be protected, a goal that will be difficult to achieve while the human population and agricultural activities continue to increase.

As elsewhere in the breeding range, Brewer's Sparrows in this region are threatened by habitat destruction and fragmentation through agricultural and urban expansion (Campbell et al. 2001). Continued livestock grazing and alteration of the natural fire cycle further threaten breeding habitat by altering the vegetation community, primarily by increasing the spread of invasive exotic plant species (Rotenberry 1998).

No previous studies of the population dynamics of Brewer's Sparrows in this region have been done. However, some information exists on breeding densities and habitat associations. Brewer's Sparrow densities averaged 5.38 males per 100 ha in twelve sites surveyed in 1991 and the estimated breeding population in the region was 413 pairs (Harvey 1992). Sarell and McGuinness (1993) estimated the population to be between 400-500 breeding pairs and reported that 48% of nests were in areas with sagebrush density from 10-30%, 32% in areas with <10% sagebrush cover and 20% in
areas with >30% sagebrush cover. Brewer's Sparrows in this region were associated with
Lupine (*Lupinus sericeus*) and Parsnip-flowered Buckwheat (*Eriogonum heracleoides*; Paczek 2002). Livestock grazing may reduce the density of such native forbs. During
the post-fledging period, juveniles moved away from the sagebrush dominated nesting
areas and used small aspen dominated gullies and areas with tall deciduous shrubs (Yu
2001). Brewer's Sparrow breeding densities in this region were lower where the density
of avian nest predators was high (Welstead 2002). Brewer’s Sparrow density was also
lower at sites with lower densities of invertebrates, which suggests that habitat selection
may be based on food availability (Krannitz unpubl.). While this information suggests
some important habitat features for Brewer's Sparrows, no information exists on which
habitat characteristics are selected at the nest-site level. Exploring which habitat
characteristics Brewer's Sparrows choose when building nests and how those are related
to nest success can increase our understanding of how habitat alteration at a fine scale
may impact productivity.

**Thesis Objectives**

My research explored the demography of the Brewer's Sparrow (*Spizella breweri*)
in southern British Columbia, a population of a declining grassland bird at the
northwestern periphery of its breeding range. I undertook a four-year, detailed
demographic study at four sites varying in habitat characteristics. This type of
demographic information is necessary to explore the causes and consequences of
population dynamics in peripheral versus core populations.

My objectives were:
1) To determine the population’s vital rates and explore causes of annual variation in those rates in relation to environmental stochasticity at a range periphery where environmental conditions may be limiting;

2) To examine the viability of a peripheral population of this declining species;

3) To explore which vital rates are most important in driving the local population dynamics; and

4) To explore nest site selection at the microhabitat scale in relation to the risk of nest predation.

I conducted this study from 1997 – 2000 in the southern Okanagan and Similkameen Valleys, British Columbia (Fig. 1.1). The study sites were situated within the Southern Interior Ecoprovince and the Okanagan Range Ecoregion of British Columbia (Demarchi 1991). All study sites were located in the shrubsteppe grasslands that are characteristic of the hot, dry aspects of the Ponderosa Pine-Bunchgrass biogeoclimatic zone (Nicholson et al. 1991). Typical vegetation consisted of Big Sagebrush shrubs (*Artemisia tridentata*) with an understory of grasses, forbs and microbiotic crust on more open ground (Tisdale 1947, Billings 1994). I selected four study sites known to support Brewer's Sparrows that varied in the degree of habitat patchiness, elevation and vegetation structure. This habitat heterogeneity allowed me to explore demographic variation in Brewer's Sparrows throughout the region.
Figure 1.1. British Columbia with inset showing study sites.
Study Sites

*Kilpoola Lake.* - The Kilpoola Lake site (KP; 20 ha, elevation 840 m) has been managed as a nature reserve since 1994 but was formerly grazed by cattle. Although the site was not actively grazed during the study, cattle from adjacent properties encroached onto the property until 1998. It was bounded on the east and west by forested ridges and had adjacent areas of similar sagebrush habitat to the north (< 15 ha) and the south (> 60 ha). The vegetation cover consisted of a fairly dense shrub layer, dominated by Big Sagebrush (*Artemisia tridentata*) and included scattered Snowberry (*Symphoricarpos albus*) and Saskatoon (*Amelanchier alnifolia*) shrubs. The understory was comprised of a mixture of native bunchgrasses, forbs, and non-native weeds on the slopes. Flatter areas were dominated by non-native Crested Wheatgrass (*Agropyron cristatum*) that was originally planted for forage.

*Schneider.* – The Schneider site (SC; 25 ha, elevation 900 m) was privately owned, grazed by horses, and was 2.5 km west of KP. The site was bordered to the north by a forested ridge and was surrounded on the other sides by areas that supported much lower densities of Brewer’s Sparrows (Mahony unpubl.). An intense wildfire removed much of the vegetation cover in the late summer of 1994. Although Big Sagebrush was returning, sage cover had not reached pre-fire density by 1997. Scattered patches of sagebrush escaped the fire; however, the dominant vegetation at the site included native bunchgrasses and forbs, non-native weeds and widely scattered shrubs, predominantly snowberry in wetter draws. This site had a much sparser overall shrub cover than the other three sites.
International Grasslands. – I began work at the International Grasslands site (IG; 15 ha, elevation 920 m) in 1998. This area was partially burned in the 1994 fire, although the section used in this study remained unburned. This site was approximately 2 km southwest of SC. The intervening area between SC and IG was burned and heavily grazed by cattle. The site was bordered to the northwest by forested ridges and to the south by large, grazed areas that straddled the Canada-US border and supported fairly high Brewer’s Sparrow densities (personal observation). The shrub cover at IG was dense and almost exclusively Big Sagebrush. The understory was similar in composition to the other sites although there tended to be more bare ground.

These three southern sites, KP, SC and IG formed a chain of high elevation habitat areas separated by 2 - 2.5 km. Densities of Brewer's Sparrows were much lower in the poorer quality habitat of the intervening areas (Mahony unpubl.).

White Lake. - The White Lake site (WL; 31 ha, elevation 400 m) was imbedded in one of the largest intact pieces of sagebrush habitat in the region, greater than 600 ha in size. This site was heavily grazed by cattle but has been managed as a nature reserve since 1995. Although some cattle grazing still occurred during the study, it took place mostly in the fall and was less intensive than before 1995. A 31 ha area where Brewer’s Sparrow density was high relative to the rest of the property was used in this study. WL was approximately 30 km north of the other three sites. The shrub layer was almost exclusively Big Sagebrush and the understory was composed of native bunchgrasses, forbs and introduced weeds.
Overview of Thesis

In this chapter, I introduced the problem of declining grassland bird populations and presented the theoretical context and mounting evidence of geographical variation in declines across the ranges of species. I described the ecology of the Brewer's Sparrow and what is known about the southern British Columbia population. This background information justifies my choice of this population as a model, peripheral population of a declining grassland bird species.

In Chapter 2, I explore spatial and temporal variation in Brewer's Sparrow productivity. I present data on daily nest survival and seasonal fecundity by site and year. I examine factors affecting seasonal fecundity including nest predation rates, the number of clutches laid, clutch size and the initiation date of the first clutch. I then examine how these factors are related to spatial and temporal variation in seasonal fecundity.

In Chapter 3, I examine annual survival and dispersal of adults and juveniles within the region. I combine these data with productivity data from Chapter Two to build a population viability model to project trends for sagebrush Brewer's Sparrows in southern British Columbia. I model two scenarios in which the mean adult survival rate and the occurrence of low survival years vary. I then explore the role of immigration in maintaining population stability and using sensitivity analysis, examine which vital rate most affects the finite population growth rate.

In Chapter 4, I test the hypothesis that Brewer's Sparrows select nesting habitat to reduce the risk of predation. First, I examine nest-site selection at the levels of the nest shrub and the 5-m radius nest patch by comparing habitat variables at nest sites to non-
nest sites. I then compare these same variables between successful and depredated nests and ask whether preferred habitat variables are also associated with nest success.

Chapter 5 summarizes my results and discusses their implications for the persistence of sagebrush Brewer's Sparrows in British Columbia. I also suggest strategies for managing this population.

Chapters 2, 3 and 4 are written as stand alone papers.

LITERATURE CITED


CHAPTER 2:

PRODUCTIVITY OF BREWER'S SPARROWS AT THE NORTHERN EDGE OF THE RANGE

ABSTRACT

I examined the proximate factors associated with seasonal fecundity in Brewer's Sparrows and explored their effects on the spatial and temporal patterns of productivity. The study took place from 1997-2000 at four sites in southern British Columbia where Brewer's Sparrows reach the northwestern edge of their breeding range.

Seasonal fecundity was highest when the rate of nest predation was low, the number of clutches/female was high and when breeding began later. It also varied between years being highest in 2000, the year with the lowest nest predation rate and intermediate number of clutches/female. Seasonal fecundity was lowest in 1998, when nest predation and the number of clutches/female were the highest and the warm El Niño conditions led to early onset of breeding. The low success, despite more clutches being laid in 1998, resulted from high levels of nest predation and an early spring storm which destroyed 43% and 20% of first nests at two high elevation sites. Because breeding began early that year, females were able to mitigate some of the early nest losses by laying more clutches.

High seasonal fecundity alternated between the sites such that the best site in 1998 became the least productive in 1999 and vice-versa, and a third site was most productive in 2000. The over-riding factor driving this spatial and temporal variation was shifting rates of nest predation, although the elevation-related storm effects and
variation in the number of clutches laid were partly responsible. These results showed that there was no consistent high vs. low, or source vs. sink sites in terms of productivity.

INTRODUCTION

Life history theory suggests that organisms make trade-offs among physiological, ecological and behavioural traits to maximize fitness (Roff 2002). Most seasonally iteroparous vertebrates maximize seasonal productivity by trading-off the costs and benefits of brood size with the number and timing of broods per season (Stearns 1976, Roff 1992). In birds, trade-offs may be made between egg size, clutch size, date of first clutch initiation and the ability of pairs to successfully fledge subsequent broods (Welty 1982, Newton 1998). Chicks from larger eggs often survive better than those from smaller eggs (Dawson and Clark 1996, Anderson and Alisauskas 2002). In a Great Tit (Parus major) population, smaller first broods were correlated with a greater likelihood of pairs raising second broods (Kluyver et al. 1977). Smith and Roff (1980) showed that Song Sparrows (Melospiza melodia) with larger broods delayed subsequent broods, indicating a cost to large early broods.

When environmental conditions are variable, birds must trade off the advantages of breeding early in the season, thereby gaining time for subsequent broods, with possible mortality of young during stochastic weather events. Populations at range peripheries may face greater environmental stochasticity as they occur at the environmental tolerance limits for the species (Maurer and Brown 1989, Shreeve et al. 1996). Therefore, birds breeding in peripheral areas of the range must invest in reproduction in unpredictable environments. Pied Flycatchers (Ficedula hypoleuca) breeding at the northern edge of
the range, where annual temperature variation was high, showed greater inter-year variation in clutch size, hatching success and fledging success than in southern populations where annual temperatures were more predictable (Järvinen 1989). Although earlier arrival dates led to increased clutch size and hatching success, annual productivity was not higher because of losses due to unpredictable weather events in the brood period (Järvinen 1994, 1995). When environmental conditions are unpredictable, there may be fitness costs and rewards to early breeding. For instance, Tree Swallow (Tachycineta bicolor) chicks produced earlier in the season were heavier and arrived earlier in subsequent years than those from later broods. However, cold weather near the time that nestlings become homeothermic often results in nestling mortality (Robertson et al. 1992).

The most common cause of reproductive failure for most songbird pairs is nest predation (Nice 1957, Lack 1966, Ricklefs 1969). In a review of the causes of nest failure for neotropical migratory songbirds, predation was the primary source of nest failure in 28 of 32 species (Martin 1992). While multi-brooded species can mitigate the effects of predation by re-nesting, their ability to do so may depend on the timing of the predation event in relation to the onset of breeding in the spring. The end of the breeding season may be fixed by the constraints of other aspects of the annual cycle such as moulting and migration.

Because multiple-brooded species maximize productivity by making trade-offs between first and subsequent broods, nesting success alone can be an inaccurate measure of annual productivity in songbirds (Thompson et al. 2001, Underwood and Roth 2002). However, accurate measures of seasonal fecundity (i.e. the total number of chicks fledged...
by females from all nesting attempts in a season) are reported rarely (Rowley and Russell 1991, Pease and Grzybowski 1995, Murray 2000; but see: Nice 1937, Nolan 1978, Haggerty 1988 and Holmes et al. 1996). Measuring seasonal fecundity in the field requires intensive effort as females must be colour-banded and followed closely through the entire breeding season to ensure that all nesting attempts are discovered. Hence, few songbird studies measure seasonal fecundity despite its importance for the demographic modeling necessary for songbird conservation (Sherry and Holmes 1999, Robinson and Morse 1999).

Population trends can be driven by variation in productivity, and declines in some songbird species have been linked to reduced fecundity (e.g., Probst 1986, Sherry and Holmes 1992, Johnson and Geupel 1996, Siriwardena et al. 2000). Therefore, determining the factors that affect annual fecundity of declining populations is a necessary step in determining the ultimate causes of decline. As a group, grassland-breeding birds have shown steeper, more persistent and geographically widespread declines than other groups of North American songbirds (Vickery et al. 1999). Despite this trend, there have been few detailed studies of the demography of these declining species (Vickery et al. 1999). A basic understanding of the demographic processes acting in declining species is key to determining the causes of decline and managing for population persistence. One such declining grassland species is the Brewer's Sparrow (Spizella breweri breweri), a multi-brooded migratory songbird that breeds in shrubsteppe grasslands throughout the Great Basin region of western North America. This species has shown a significant range-wide decline of 3% per year from 1966-2000 according to Breeding Bird Survey (BBS) data (Sauer et al. 2001). The causes of decline
are thought to include fragmentation and loss or alteration of shrub-steppe breeding habitat (Rotenberry et al. 1999). In Washington, nest predation rates of four shrub-steppe breeding passerines, including Brewer’s Sparrows, were higher in fragmented versus continuous patches of sagebrush habitat (Vander Haegen et al. 2002).

Brewer’s Sparrows reach the extreme northwestern limit of their breeding range in the southern interior of British Columbia. I assessed the productivity of Brewer’s Sparrows from 1997-2000 at four sites in this region. My objectives were to examine the proximate factors determining seasonal fecundity and to explore the spatial and temporal variation in productivity. I hypothesized that productivity would be most affected by levels of nest predation and the rate of re-nesting after failed and successful nests. I also hypothesized that the date of onset of breeding would affect fecundity through increased number of nest attempts in early vs. late years and that therefore, fecundity would vary with season length. Seasonal fecundity was therefore predicted to be highest when and where nest predation rates were low and in years when nesting began early. Because the sites differed in elevation, habitat structure and patch size, I predicted that seasonal fecundity would be higher in the larger patch, at lower elevation and where sagebrush cover was more dense, than at isolated, higher elevation sites and where wildfire had reduced sagebrush cover.
METHODS

Field Methods

I conducted this study from 1997 – 2000 at four sites in the southern Okanagan and Similkameen Valleys, British Columbia (see Chapter 1).

Capture and Banding.- I captured breeding birds in mist-nets and gave them unique colour band combinations using two or three colour bands and one aluminium Canadian Wildlife Service number band. In 1997, I began mist-netting in early May at three sites (KP, SC, WL) and continued until mid-June (capturing as many breeding birds as possible). Nets were erected near singing male perches and song playback was used to draw birds into mist-nets. I banded birds at all four sites from 1998-2000, although the focus shifted to capturing breeding females after 1997. I began mist-netting with the onset of nesting and continued until a minimum of 12 breeding females were banded at each site. Nets were placed near (5-10 m) active nests and birds were either flushed directly off nests into the mist-nets if incubating or brooding, or were captured as they returned to the nest.

Nest Searching and Monitoring.- I began nest searching in early May and continued until nesting activities were completed at the end of July each year. Nests were located by intensive searching, usually in the area of a singing male, and often by following females carrying nesting material, or flushing birds from nests. I searched all areas of the study sites at the beginning of the breeding season but efforts were concentrated on following colour-banded females later in the season to determine the outcomes of all nesting attempts. Flagging tape marked with the bearing and distance of
the nest was placed 15 – 25 m away from each nest to mark its location. I monitored all nests by checking them every three to five days until they failed or fledged. To reduce observer-induced predation effects, nests were approached from different angles on each visit and examination of nest contents was as inconspicuous as possible. Numbers of eggs or chicks and the age of chicks (based on size and feather development) were recorded at each visit. I determined clutch initiation dates for those nests found during laying. For nests discovered after incubation began, I estimated clutch initiation dates by back-dating once the eggs had hatched (using 11 days for incubation beginning when the penultimate egg was laid; Rotenberry et al. 1999). For nests found after hatching, chicks were aged by size and development. This allowed me to estimate hatching and fledging dates (chicks fledge at 8 – 9 days; Rotenberry et al. 1999). To estimate brood size at fledging, nests were checked as close to the estimated fledging date as possible, usually within 1-3 days.

I recorded a nest as successful if it was empty soon after the expected fledge date and if fledged chicks, adults with food, or agitated adults were observed near the nest. The number of fledglings was assumed to be the number of chicks observed in the nest on the last visit prior to fledging, minus any dead ones in or near the nest. I considered this assumption reasonable as partial predation of broods was rare (4 % of nests with chicks) and because nests were checked near to fledging. I considered a nest to have been depredated if it was empty prior to the estimated fledge date, if there was no evidence that early fledging took place, or if it contained dead chicks with obvious signs of attack or broken eggshells. I also recorded nests as depredated if they were found empty and intact after the expected fledge date if three subsequent visits failed to provide
evidence of fledglings on the territory. This assumption was reasonable since pairs with young fledglings remained on the territory for over a week, and appeared agitated and called to fledglings when approached by an observer. In contrast, pairs whose nests were depredated were less conspicuous and did not respond to the presence of observers. I considered nests to have been abandoned if a full or partial clutch did not hatch by a few days after the calculated hatch date and/or eggs were cold and wet with no breeding adults in attendance. Some nests failed when chicks were found dead in nests after periods of heavy rain and below average temperatures. I excluded from analysis any nests that were found empty and remained empty upon subsequent checks, because it was not known whether they had been abandoned or depredated between checks. I recorded the presence of Brown-headed Cowbird (*Molothrus ater*) eggs or chicks in nests, as nest parasitism by cowbirds can reduce songbird productivity (Robinson et al. 1995).

**Statistical Analyses**

*Daily Survival Rates.* I considered nests to have been successful if at least one chick fledged. I calculated daily survival rates and their standard errors for nests using Bart and Robson's method (1982). Estimates were calculated for the entire nesting period from the onset of incubation: 11 days for incubation plus 8 days to fledging. I explored site*year interactions using the program CONTRAST (Sauer and Williams 1989) to test the null hypotheses that daily nest survival values did not vary between sites within years and between years at given sites. I then made multiple comparisons between sites within years and between years within sites using the Bonferroni adjustment (*α* = 0.05 / # comparisons) to determine alpha levels (Neter et al. 1996).
Seasonal Fecundity. - Brewer's Sparrows are multi-brooded, readily re-nesting after both failed and successful early nests (Rotenberry et al. 1999, Mahony et al. 2001). Therefore, I used a sub-set of nests belonging to colour-banded females, to measure seasonal fecundity at each site from 1998 - 2000. I followed colour-banded females closely throughout the breeding season to estimate the number of nesting attempts made by each female and the outcomes of each attempt. I recorded the total number of chicks fledged during all nesting attempts by a female in a given season. In a few cases (8 of 173), banded females were observed with fledged young, usually from second or third attempts for which the nest was not found. In these cases, I estimated the number of fledged young from that attempt as the mean number of young fledged per successful nest (3.54 for first attempts, 2.95 for subsequent ones) and the resulting seasonal total was rounded to the nearest whole number.

Twenty-two of the 173 individual females examined were encountered in two years of the study. I randomly selected and removed from the dataset one of the years in which these females were encountered, since repeated measures could bias mean fecundity values.

The number of chicks fledged in a breeding season is the product of the number of clutches laid, the clutch sizes, and the proportion of those eggs laid that result in fledglings. I hypothesized that seasonal fecundity was influenced by the onset of breeding in the spring, as earlier nesting would allow more time for subsequent nest attempts. I also hypothesized that seasonal fecundity would vary between sites depending on habitat quality, and between years depending on weather conditions. To determine the influence of each factor on productivity, I used a regression approach. In
this way, I was able to test which factors most influenced seasonal fecundity. The factors included in the regression model were, for each female: number of clutches laid, mean clutch size, proportion of all eggs laid that were lost to predation, date of initiation of first clutch, site and year. Nest parasitism was not included in the model as Brown-headed Cowbirds parasitized only 3.5% of nests. Occasionally, I was unable to determine a clutch size if a nest was discovered at the nestling stage, or if it was found with an incomplete clutch that was depredated before it was next checked. In these cases (6.1%), mean values of 3.89 eggs, 3.65 eggs and 3.46 eggs were assigned for first, second and subsequent clutches and the resulting total number of eggs was rounded to the nearest whole number.

Count data, such as the number of fledged chicks, are more likely to follow a Poisson than a normal distribution (McCullagh and Nelder 1989). Poisson regression is a log-linear model where expected values of the dependent variable are a log-linear function of the explanatory variables (Allison 1991, Gardner et. al. 1995). I employed Poisson regression in the GENMOD procedure of SAS to model the relationship between seasonal fecundity and the proximate factors listed above (Allison 1991, SAS version 8; SAS Institute Inc. 1999). Wald statistics were calculated to analyze parameter estimates (β) for predictor variables and Type III likelihood ratio statistics were calculated to test the significance of the predictor variables (Allison 1991). The model fit was assessed by dividing the deviance (-2log likelihood) by the degrees of freedom (Allison 1991). To explore the predictive ability of each independent variable, the percentage change in expected seasonal fecundity with each 1-unit change in the independent variable was calculated using the formula 100(e^β - 1) (Allison 1991).
I used an ANOVA approach to further explore the spatial and temporal variation in seasonal fecundity. Due to non-normality of seasonal fecundity data, I used the non-parametric rank method in the GLM procedure of SAS to compare the main effects site, year and the site*year interaction on number of chicks per female (version 8; SAS Institute Inc. 1999). The ranking procedure was considered valid as general linear models are robust to small deviations from normality and, after data were ranked, they were normal or close to normal for all comparisons (Neter et al. 1996). I made comparisons between sites for each year and between years for each site. These multiple comparisons were accomplished using the LSMEANS procedure in SAS, employing Bonferroni adjustments for alpha levels. When these comparisons were significant, univariate comparisons were made between the number of clutches laid, mean clutch size, the rate of nest predation and date of onset of breeding to explain the variation in seasonal fecundity.

RESULTS

Of the 657 nests I located at all four sites, over half were successful, fledging at least one chick. The most common cause of nest failure was predation, followed by abandonment and destruction in storms (Table 2.1). Mean clutch size was 3.76 ± 0.02 (S.E., n = 516) and mean brood size of successful nests was 3.27 ± 0.04 (S.E., n = 482).

Daily Nest Survival Rate

The mean daily nest survival rate during the study was 0.957, corresponding to a survival rate of 0.434 for the entire 19 day nest period. Daily nest survival varied across
years of the study ($X^2 = 9.81$, $P = 0.002$, df = 3) being lower in 1998, when breeding began earliest and nest predation was highest, than in 2000 ($X^2 = 9.76$, $P = 0.002$, df = 1, Table 2.1). Daily nest survival also varied between sites ($X^2 = 7.97$, $P = 0.05$, df = 3) being lower at WL, where predation was highest, than at IG and SC ($X^2 = 6.4$, $P = 0.01$, df = 1, Table 2.1).

### Table 2.1. Nest fates and daily nest survival rates of Brewer’s Sparrow nests at four sites in the southern Okanagan and Similkameen Valleys, B.C. 1997-2000, (*a* data not collected at IG in 1997).

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>% Nests Successful (≥ 1 chick fledged)</th>
<th>% Nests lost to Predation</th>
<th>% Nests Abandoned</th>
<th>% Nests lost to Storms</th>
<th>Daily Survival Rate ± (S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997*</td>
<td>90</td>
<td>56.7</td>
<td>35.3</td>
<td>6.9</td>
<td>2.1</td>
<td>0.958 (.010)</td>
</tr>
<tr>
<td>1998</td>
<td>249</td>
<td>43.4</td>
<td>43.0</td>
<td>5.4</td>
<td>8.1</td>
<td>0.948 (.004)</td>
</tr>
<tr>
<td>1999</td>
<td>169</td>
<td>56.2</td>
<td>39.9</td>
<td>3.3</td>
<td>0.7</td>
<td>0.955 (.010)</td>
</tr>
<tr>
<td>2000</td>
<td>149</td>
<td>58.4</td>
<td>36.6</td>
<td>3.9</td>
<td>0.0</td>
<td>0.968 (.005)</td>
</tr>
<tr>
<td>Site</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>KP</td>
<td>196</td>
<td>45.9</td>
<td>50.6</td>
<td>3.3</td>
<td>0.8</td>
<td>0.953 (.007)</td>
</tr>
<tr>
<td>SC</td>
<td>175</td>
<td>58.9</td>
<td>27.0</td>
<td>4.7</td>
<td>5.9</td>
<td>0.965 (.009)</td>
</tr>
<tr>
<td>IG</td>
<td>105</td>
<td>59.0</td>
<td>29.4</td>
<td>6.5</td>
<td>4.4</td>
<td>0.965 (.003)</td>
</tr>
<tr>
<td>WL</td>
<td>181</td>
<td>47.5</td>
<td>46.4</td>
<td>4.9</td>
<td>0.4</td>
<td>0.948 (.006)</td>
</tr>
<tr>
<td>Mean</td>
<td>657</td>
<td>53.6</td>
<td>38.9</td>
<td>4.7</td>
<td>2.8</td>
<td>0.957 (.004)</td>
</tr>
</tbody>
</table>

Within sites, daily nest survival varied between years. For example, at KP it was lower in 1998 than 1999 ($X^2 = 6.92$, $P = 0.008$, df = 1), corresponding to the large difference in predation rates between the years (Fig. 2.1). At SC, it varied across years ($X^2 = 15.93$, $P = 0.001$, df = 3) and was lower in 1998, when predation rate and the proportion of nests lost in storms were high, compared to 1997 and 2000 (Fig. 2.1). There were no significant differences in daily nest survival between years at either WL or IG.
Daily nest survival varied between sites in 1999 and 2000, but not in 1997 or 1998. In 1999, the daily nest survival at KP was significantly higher than at WL ($X^2 = 7.09, P = 0.008, df=1$) where the predation rate was almost twice as high (Fig. 2.1). In 2000, daily nest survival at SC was higher than at WL ($X^2 = 13.08, P = 0.003, df=1$) where the predation rate was more than three times as high (Fig. 2.1).

Figure 2.1. Causes of failure of Brewer’s Sparrow nests at four sites in the southern Okanagan and Similkameen Valleys, B.C. 1997-2000 (data not collected at IG in 1997).
Seasonal Fecundity

Mean seasonal fecundity of 151 females was $3.02 \pm 0.20$ (S.E.) and ranged from 1.2 fledglings per female at KP in 1998 to 4.7 fledglings per female at SC in 2000. The maximum seasonal fecundity recorded was ten fledglings reared by a single female from three nests at KP in 1999 (Mahony et al. 2001).

Correlates of Seasonal Fecundity. - The Poisson regression model was a good fit to the data as deviance (136.9) divided by the degrees of freedom (142) was close to one (0.97; Allison 1991, Gardner et al. 1995). The best predictors of seasonal fecundity were predation rate ($P < 0.001$) and the number of clutches laid ($P < 0.001$; Table 2.2). For each 1% increase in nest predation rate, seasonal fecundity decreased by 2.3% and for each additional clutch laid, seasonal fecundity increased by 107%. Forty-three % of 151 females laid only one clutch, 48% laid two, 8% laid three and 1% laid four clutches in a season. Seventeen percent of females successfully raised two broods in a season and two females raised three broods (Mahony et al. 2001).

There was a trend toward higher seasonal fecundity with later initiation dates; contrary to the prediction, however, the relationship was not significant ($P = 0.067$, Table 2.2). For each day that the onset of breeding was delayed, fecundity increased by 1.3%. Mean May temperature was higher in 1998 than in 1999 and 2000, leading to earlier onset of breeding in that year (Table 2.3). However, there was a cost associated with this early breeding when a three-day storm during the third week of May with low temperatures ($4^\circ C$ at 11 AM at KP) and high rainfall caused the loss by exposure of 18% of all first nests in 1998 (Table 2.3). Breeding began later in subsequent years with negligible nest losses due to exposure.
Table 2.2. The relationship between Brewer's Sparrow seasonal fecundity and six predictor variables as estimated by Poisson regression analysis.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>DF</th>
<th>Estimate</th>
<th>Chi-Square</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>1</td>
<td>-2.123</td>
<td>1.17</td>
<td>0.070</td>
</tr>
<tr>
<td>Site KP</td>
<td>1</td>
<td>-0.085</td>
<td>0.39</td>
<td>0.533</td>
</tr>
<tr>
<td>SC</td>
<td>1</td>
<td>-0.299</td>
<td>4.82</td>
<td><strong>0.028</strong></td>
</tr>
<tr>
<td>IG</td>
<td>1</td>
<td>-0.140</td>
<td>1.01</td>
<td>0.315</td>
</tr>
<tr>
<td>WL</td>
<td>0</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td>YEAR 1998</td>
<td>1</td>
<td>-0.381</td>
<td>7.43</td>
<td><strong>0.006</strong></td>
</tr>
<tr>
<td>1999</td>
<td>1</td>
<td>-0.227</td>
<td>3.43</td>
<td>0.064</td>
</tr>
<tr>
<td>2000</td>
<td>0</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
<tr>
<td># Clutches</td>
<td>1</td>
<td>0.730</td>
<td>72.64</td>
<td><strong>0.001</strong></td>
</tr>
<tr>
<td>% Eggs Predated</td>
<td>1</td>
<td>-2.277</td>
<td>136.51</td>
<td><strong>0.001</strong></td>
</tr>
<tr>
<td>Date 1st Nest Initiated</td>
<td>1</td>
<td>0.013</td>
<td>3.41</td>
<td>0.065</td>
</tr>
<tr>
<td>Mean Clutch Size</td>
<td>1</td>
<td>0.249</td>
<td>2.92</td>
<td>0.087</td>
</tr>
</tbody>
</table>

Likelihood Ratio Statistics for Type III Analysis

<table>
<thead>
<tr>
<th>Parameter</th>
<th>DF</th>
<th>Chi-Square</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
<td>3</td>
<td>5.27</td>
<td>0.153</td>
</tr>
<tr>
<td>Year</td>
<td>2</td>
<td>9.33</td>
<td><strong>0.009</strong></td>
</tr>
<tr>
<td># Clutches</td>
<td>1</td>
<td>73.45</td>
<td><strong>0.001</strong></td>
</tr>
<tr>
<td>% Eggs Predated</td>
<td>1</td>
<td>189.67</td>
<td><strong>0.001</strong></td>
</tr>
<tr>
<td>Date 1st Nest Initiated</td>
<td>1</td>
<td>3.37</td>
<td>0.067</td>
</tr>
<tr>
<td>Mean Clutch Size</td>
<td>1</td>
<td>2.95</td>
<td>0.089</td>
</tr>
</tbody>
</table>

There was also a trend towards higher fecundity with increased clutch size, but the relationship was not significant ($P = 0.089$, Table 2.2). Females that laid an average of one extra egg per clutch, increased their seasonal fecundity by 28.3%. Clutch size decreased over the course of the season, averaging 3.89 eggs for first nests, 3.65 eggs for second nests and 3.46 eggs for subsequent ones. Thus, the loss of early nests may have been more costly in terms of seasonal fecundity than were later nest losses.
Table 2.3. Brewer’s Sparrow nest losses to storms in relation to the date of first clutch initiation and mean May temperature in the southern Okanagan and Similkameen Valleys, B.C. from 1998-2000.

<table>
<thead>
<tr>
<th>Year</th>
<th>Mean May Temp(°C)</th>
<th>Mean Date 1st Nest Initiated</th>
<th>% 1st nests lost in storms</th>
</tr>
</thead>
<tbody>
<tr>
<td>1998</td>
<td>16.8</td>
<td>May 12</td>
<td>18</td>
</tr>
<tr>
<td>1999</td>
<td>13.3</td>
<td>May 29</td>
<td>2</td>
</tr>
<tr>
<td>2000</td>
<td>14.2</td>
<td>May 22</td>
<td>0</td>
</tr>
</tbody>
</table>

*Data from Environment Canada weather station at Osoyoos B.C.*

Seasonal fecundity varied with year; it was lower in 1998 than in 2000 (Table 2.2, Fig. 2.2). The number of clutches was actually lower in 2000 than in 1998 ($P = 0.016$), despite the higher fecundity (Table 2.4). However, the earlier onset of breeding in 1998 than in 2000 ($P = 0.001$) that was associated with early nest losses in a storm was partly responsible for the difference in fecundity (Table 2.4).

Figure 2.2. Variation in Brewer’s Sparrow seasonal fecundity in the southern Okanagan and Similkameen Valleys, B.C., 1998-2000. Different letters above bars denote significant differences between years.
The difference in the nest predation rate between 1998 and 2000 was not significant \((P = 0.15)\) suggesting that early nest losses to storms were more important than nest predation in 1998 (Table 2.4). Re-nesting after these early losses accounted for the higher number of clutches laid in 1998. Hence, although more clutches were laid, due to storm losses, the success of those clutches was lower.

**Table 2.4.** Factors contributing to variation in seasonal fecundity of female Brewer’s Sparrows from 1998-2000 at four sites in southern Okanagan and Similkameen Valleys, B.C. N = the number of females.

<table>
<thead>
<tr>
<th>Year – Site</th>
<th>N</th>
<th>chicks/ female</th>
<th># clutches</th>
<th>clutch size</th>
<th>% depredated</th>
<th>date 1st nest initiated</th>
<th>% 1st nests lost in storm</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1998</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>all sites</td>
<td>54</td>
<td>2.57</td>
<td>1.81</td>
<td>3.87</td>
<td>37.1</td>
<td>May 12</td>
<td>18.0</td>
</tr>
<tr>
<td>KP</td>
<td>13</td>
<td>1.23</td>
<td>1.61</td>
<td>3.91</td>
<td>69.5</td>
<td>May 12</td>
<td>7.1</td>
</tr>
<tr>
<td>SC</td>
<td>15</td>
<td>2.93</td>
<td>2.00</td>
<td>3.84</td>
<td>19.0</td>
<td>May 12</td>
<td>43.8</td>
</tr>
<tr>
<td>IG</td>
<td>13</td>
<td>2.23</td>
<td>1.61</td>
<td>3.91</td>
<td>24.1</td>
<td>May 15</td>
<td>20.0</td>
</tr>
<tr>
<td>WL</td>
<td>13</td>
<td>3.85</td>
<td>2.00</td>
<td>3.85</td>
<td>35.9</td>
<td>May 15</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>1999</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>all sites</td>
<td>51</td>
<td>2.84</td>
<td>1.55</td>
<td>3.82</td>
<td>36.1</td>
<td>May 29</td>
<td>2.0</td>
</tr>
<tr>
<td>KP</td>
<td>15</td>
<td>4.13</td>
<td>1.80</td>
<td>3.88</td>
<td>30.9</td>
<td>May 28</td>
<td>0.0</td>
</tr>
<tr>
<td>SC</td>
<td>9</td>
<td>2.56</td>
<td>2.00</td>
<td>3.61</td>
<td>32.9</td>
<td>June 1</td>
<td>9.0</td>
</tr>
<tr>
<td>IG</td>
<td>10</td>
<td>3.20</td>
<td>1.20</td>
<td>3.83</td>
<td>23.8</td>
<td>May 30</td>
<td>0.0</td>
</tr>
<tr>
<td>WL</td>
<td>17</td>
<td>1.65</td>
<td>1.18</td>
<td>3.88</td>
<td>56.7</td>
<td>May 29</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>2000</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>all sites</td>
<td>46</td>
<td>3.74</td>
<td>1.68</td>
<td>3.78</td>
<td>28.2</td>
<td>May 22</td>
<td>0.0</td>
</tr>
<tr>
<td>KP</td>
<td>13</td>
<td>4.00</td>
<td>1.77</td>
<td>3.83</td>
<td>37.5</td>
<td>May 23</td>
<td>0.0</td>
</tr>
<tr>
<td>SC</td>
<td>10</td>
<td>4.70</td>
<td>1.80</td>
<td>3.75</td>
<td>9.3</td>
<td>May 20</td>
<td>0.0</td>
</tr>
<tr>
<td>IG</td>
<td>9</td>
<td>3.89</td>
<td>1.78</td>
<td>3.61</td>
<td>23.3</td>
<td>May 22</td>
<td>0.0</td>
</tr>
<tr>
<td>WL</td>
<td>14</td>
<td>2.71</td>
<td>1.36</td>
<td>3.86</td>
<td>42.7</td>
<td>May 21</td>
<td>0.0</td>
</tr>
<tr>
<td><strong>Overall</strong></td>
<td>151</td>
<td>3.02</td>
<td>1.68</td>
<td>3.83</td>
<td>33.8</td>
<td>May 22</td>
<td>6.7</td>
</tr>
</tbody>
</table>

Although regression analysis demonstrated that seasonal fecundity was not correlated with site, it appeared that this was the result of high seasonal fecundity alternating between sites from year to year; so further examination of the interaction of spatial and temporal variation was warranted (Table 2.4).
Spatial and Temporal Patterns of Seasonal Fecundity. – There was a significant year effect on seasonal fecundity and the site*year interaction was significant (Table 2.5). Seasonal fecundity was highest at WL in 1998, the site at which it was lowest in the following two years. KP showed the opposite pattern, with fecundity being lowest in 1998, highest in 1999 and second highest in 2000 (Fig. 2.3). Significant differences in seasonal fecundity occurred between sites in 1998 and 1999 and between the years of the study at KP and WL (Fig. 2.3).

Table 2.5. Two-way ANOVA comparing Brewer’s Sparrow seasonal fecundity (# chicks/female) in the southern Okanagan and Similkameen Valleys, B.C. 1998-2000, between years and sites and showing the year*site interaction.

<table>
<thead>
<tr>
<th></th>
<th>d.f.</th>
<th>Type III SS</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model</td>
<td>11</td>
<td>160.42</td>
<td>14.58</td>
<td>2.65</td>
<td>0.004</td>
</tr>
<tr>
<td>Year</td>
<td>2</td>
<td>41.00</td>
<td>20.50</td>
<td>3.73</td>
<td><strong>0.027</strong></td>
</tr>
<tr>
<td>Site</td>
<td>3</td>
<td>8.45</td>
<td>2.81</td>
<td>0.51</td>
<td>0.675</td>
</tr>
<tr>
<td>Year*Site</td>
<td>6</td>
<td>111.47</td>
<td>18.58</td>
<td>3.38</td>
<td><strong>0.004</strong></td>
</tr>
<tr>
<td>Error</td>
<td>139</td>
<td>764.52</td>
<td>5.50</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Changes in predation rates and the number of clutches laid drove the observed spatial differences in seasonal fecundity. In 1998, seasonal fecundity was lower at KP than at WL, when there were trends toward a higher predation rate ($P = 0.09$) and fewer clutches laid ($P = 0.08$), although neither was significantly different (Table 2.4). These differences may not have been significant due to the small number of females sampled at a given site in one year. Despite 43% of first nests being lost in the storm at SC, fecundity was not significantly different at SC than at WL in 1998. By re-laying after these early losses, females at SC laid as many clutches as at WL, and with a lower predation rate, more of their nesting attempts were successful (Table 2.4). At IG, 20% of
first nests were lost in the 1998 storm and fewer of these nests were replaced, which led to marginally lower fecundity than at WL, although the difference was not significant, possibly due to small sample sizes ($P = 0.08$; Table 2.4). The effect of the storm varied with elevation as there were no nest losses during the storm at WL (400 m), the lowest elevation site, but losses were large at SC (900 m) and IG (920 m). In 1999, the most and least productive sites were reversed, with KP having significantly higher fecundity than WL ($P = 0.003$; Fig. 2.3). This was primarily a result of more clutches being laid at KP ($P = 0.001$) than at WL (Table 2.4). Although differences in seasonal fecundity between sites were not significant in 2000, it is worth noting that females at SC had the highest fecundity, laid the most clutches and had the lowest nest predation rate (Table 2.4).

Figure 2.3. Seasonal fecundity (# fledglings/female) at four sites in the southern Okanagan and Similkameen Valleys, B.C. 1998-2000 (different upper case letters denote significant within-year comparisons $\alpha \leq 0.008$, Fisher’s LSD test; different lower-case letters denote significant within-site comparisons $\alpha \leq 0.01$, Fisher’s LSD test).
The overriding effects of variation in predation rates and the number of clutches on seasonal fecundity were shown by the temporal patterns of changes in seasonal fecundity within sites. At KP, fecundity was higher in 2000 than in either 1998 ($P = 0.001$) or 1999 ($P = 0.003$) when predation rates were almost twice as high (Fig. 2.3, Table 2.4). At WL, fecundity was higher in 1998 when the number of clutches was almost double than in 1999 ($P = 0.01$; Table 2.4, Fig. 2.3). The number of clutches laid was higher at WL in 1998, the early season than in either 1999 or 2000 ($P = 0.001$).

**Brown-headed Cowbird Parasitism.** Nest parasitism by Brown-headed Cowbirds was infrequent, averaging 3.5% of nests (range: 0 – 11.5%). Of the 22 nests parasitized during the study, six were abandoned during incubation; 12 had cowbird eggs that did not hatch; three nests were depredated before hatching; and one nest fledged four sparrows and one cowbird.

**DISCUSSION**

Trade-offs made between the timing of breeding, clutch size and number of clutches laid affect annual productivity (Stearns 1976, Roff 1992). Where environmental and ecological conditions are highly variable, annual productivity of populations is likely to be highly variable and may depend on how reproductive trade-offs are made (Maurer and Brown 1989, Shreeve *et al.* 1996, Orzack and Tuljapurkar 2001). Seasonal fecundity in Brewer's Sparrows at the northern edge of the range fluctuated between years with variation in the rate of nest predation, the number of clutches laid and the timing of breeding. Spatio-temporal interaction in seasonal fecundity resulted from stochastic fluctuations in rates of nest predation across sites and the differential effects of timing of
breeding and number of clutches laid at different elevations. Annual variation in
Brewer’s Sparrow productivity has been observed in other regions. In Idaho, daily nest
survival ranged from 0.93 to 0.99 over 5 years (Petersen and Best 1987). In Oregon, the
number of Brewer’s Sparrow fledglings per nest was highly correlated with the amount
of precipitation the preceding winter and ranged from 1.79 - 3.38 chicks between dry and
wet years (Rotenberry and Wiens 1991). No other study has reported on seasonal
fecundity in Brewer’s Sparrows.

Factors Influencing Annual Variation in Seasonal Fecundity

Annual fluctuation in productivity is a common feature of songbird demography
and often is the result of annual changes in food abundance, weather patterns or predator
Most nest failure in open-cup nesting songbirds is caused by predation (Nice 1957,
Ricklefs 1969, Martin 1992). Seasonal fecundity in this study was strongly affected by
nest predation, which was the predominant cause of nest failure. Fecundity was highest
in 2000 when the predation rate was lowest, and was lowest in 1998 when predation was
highest. The 39% rate of nest predation I found was close to the 43% rate reported for 32
species of neotropical migrants by Martin (1992). Other studies have shown
considerable geographic variation in Brewer’s Sparrow nest predation rates: 11% in
Oregon (Rotenberry and Wiens 1989) to 86% in Idaho (Reynolds 1981). This suggests
that variation in site-level abundances of predators, or abundances of alternative food
supplies for those predators may be responsible.
An artificial nest study in Brewer's Sparrow habitat in this region found that nest predators included Common Ravens (*Corvus corax*), American Crows (*Corvus brachyrhynchos*), Black-billed Magpies (*Pica pica*) and small mammals (Welstead 2002). A garter snake (*Thamnophis elegans*) was observed in a nest eating Brewer’s Sparrow chicks at KP during this study. Independent population fluctuations of this diverse suite of predators, were likely responsible for the stochastic annual changes in the rate of predation on Brewer's Sparrow nests. Fluctuation in productivity resulting from annual variation in predation rates has been observed in many species: *e.g.*, Red-winged Blackbirds (*Agelaius phoenicius*; Orians and Beletsky 1989), Song Sparrows (Arcese *et al.* 1992), and Woodpigeons (*Columba palumbus*; Murton *et al.* 1964).

Female Brewer's Sparrows were able to mitigate the cost of early nest losses by re-nesting. For this reason, the number of clutches laid by a female in a season was a strong predictor of her seasonal fecundity. Despite this, I observed the counterintuitive result that the mean annual fecundity was significantly higher in 2000 when fewer clutches were laid than in 1998. Although many first nests were lost in a storm and to a high level of nest predation in 1998, there was time left in the season to make further nesting attempts because breeding began early. This replacement of early failed nests accounts for the discrepancy between the high number of clutches laid and low fecundity in 1998; more clutches were laid, but fewer were successful. In fact, 73% of females that laid three clutches in a season during the study did so in 1998, the early breeding season.

The effect of nest losses on annual productivity can vary depending on when during the breeding season the loss occurs. First clutches and broods were on average larger than subsequent ones meaning that the loss of first nests may have been more
costly, as replacement nests resulted in fewer fledglings. This is a common pattern in birds as a female’s physiological ability to produce subsequent broods may be related to the size of her initial brood (Nilsson 2000, Visser and Lessells 2001). For example, in Great Tits, smaller first broods were correlated with a greater likelihood of pairs raising second broods (Kluyver et al. 1977). Smith and Roff (1980) showed that Song Sparrows (Melospiza melodia) with larger broods delayed subsequent broods, indicating a cost to large early broods. Whether there was time left in the season to re-nest depended to some extent on when breeding began in the spring. Nests lost later in the season were unlikely to be replaced as there may not have been time for chicks to be fledged before the constraints of moult ing and migration took place.

Contrary to my prediction, early onset of breeding in this study was not associated with higher productivity in this study, largely as a result of early nest losses to the storm. Other studies found that early breeding can increase productivity by allowing multiple nesting attempts or by differentially greater success of early nests. Nest success in Mourning Doves (Zenaida macroura, Miller et al. 2001) and Pied Flycatchers (Ficedula hypoleuca, Järvinen and Väisänen 1984) was higher in warm/dry springs when breeding began earlier. Eastern Kingbird (Tyrannus tyrannus) fledgling production was higher in early initiated clutches (Blancher and Robertson 1985) and later clutches were smaller (Murphy 1986). Snow Geese (Chen caerulescens) that delay breeding when snowmelt is late have smaller clutch sizes than when breeding begins earlier (Davies and Cooke 1983). However, there is often a trade-off between the advantages of breeding early and the risk of nest losses to stochastic weather events, as was observed in this study. Tree Swallow (Tachycineta bicolor) chicks produced earlier in the season were heavier and
arrived earlier in subsequent years than those from later broods. However, cold weather near the time that nestlings were becoming homeothermic often results in nestling mortality (Robertson et al. 1992). Alpine birds that are adapted to harsh conditions have other strategies to trade-off the costs and benefits of reproduction. During a harsh breeding season, female White-tailed Ptarmigan (*Lagopus leucurus*) started breeding in poor condition but compensated by taking more incubation recesses (Wiebe and Martin 2000).

The trade-off between early breeding and the risk of weather-related mortality may be even more extreme where a species is close to its environmental tolerance limits, such as near latitudinal or altitudinal limits (Wingfield 1988, Martin 2001). Rotenberry et al. (1999) reported no other cases of nestling death attributed to exposure in Brewer’s Sparrows from elsewhere in the breeding range. This suggests that the effect of environmental stochasticity on Brewer’s Sparrow productivity may be greater in British Columbia, at the northern edge of the range, and especially where they breed at higher elevations within this region. Pied Flycatchers (*Ficedula hypoleuca*) breeding at the northern edge of the range where annual temperature variation was high showed greater inter-year variation in clutch size, hatching success and fledging success than in southern populations where annual temperatures were more predictable (Järvinen 1989). Although earlier arrival dates in warm years led to increased clutch size and hatching success, annual productivity was not higher because of losses due to unpredictable weather events in the brood period (Järvinen 1994, 1995).

The mild spring temperature and consequent early start to the breeding season in 1998 was associated with the 1997-98 El Niño event, which was followed by the cool, La
Niña spring of 1999 when breeding was delayed by three weeks from the previous year. If the storm had not caused early nest losses, 1998 may have been the most productive year as early breeding would have lead to more nesting attempts and higher fecundity. This was precisely the case at WL, the site where only one nest was lost in the storm; more clutches were laid and fecundity was highest in 1998. Nott et al. (2002) found that productivity of neotropical migrants wintering in western Mexico and breeding in the Pacific Northwest was higher in summers following an El Niño winter. Similarly, Rufous-crowned Sparrow and Bridled Titmouse (Baeolophus wollweberi) productivity were highest in an El Niño year and lowest in the following La Niña year (Morrison and Bolger 2002, Christman 2002, respectively). Favoured early season nesting conditions and low rates of nest predation allowed for multiple-brooding leading to higher seasonal fecundity in the El Niño year, mirroring the pattern seen in this study at WL. However, Rotenberry and Wiens (1991) did not find a close link between large-scale weather patterns and shrubsteppe bird productivity. They suggested that this may be related to time lags in predator response to such weather patterns.

Recent reports have linked earlier arrival of spring migrants and earlier egg-laying dates over the last few decades to temperature increases due to climate change (e.g. Crick et al. 1997, Crick and Sparks 1999, Dunn and Winkler 1999, Hüppop and Hüppop 2003). This may allow birds to increase annual productivity by laying more clutches, unless the early breeding leads to mistiming between the onset of breeding and peaks in food resources (Visser et al. 1998, Inouye et al. 2000). However, climate change models predict increases in unpredictable, extreme weather events such as storms (IPCC 2001). Under such a scenario, early breeders will have to trade off the advantages
and disadvantages of early nesting on productivity. This study demonstrated such a trade-off when early breeding in 1998 led to nests losses in an unusual storm in that year. In 1999 and 2000, when breeding began two to three weeks later, fewer clutches were laid but nest losses to storms were negligible.

Spatial and Temporal Interaction in Seasonal Fecundity

Seasonal fecundity did not vary between the sites over all the years of the study. However, there was a significant spatio-temporal interaction because site-related productivity alternated between years with the best site becoming the least productive and vice-versa. Many studies of birds have shown spatial variation in productivity (Lack 1966, Nolan 1978, Blancher and Robertson 1985, Donovan et al. 1995, Holmes et al. 1996, Smith et al. 1996, Paradis et al. 2000, Vierling 2000, Saab and Vierling 2001). However, in these studies, productivity remained high in the same areas year after year and was related to habitat differences between the sites. For example, Black-throated Blue Warbler (Dendroica caerulescens) productivity was consistently higher year after year where shrub density was higher (Holmes et al. 1996). Source-sink population theory suggests that movements from consistent source habitats support, through immigration, sink populations that do not produce enough young to be self-sustaining (Pulliam 1988). Saab and Vierling (2001) showed that Lewis’s Woodpecker (Melanerpes lewis) productivity was consistently higher in burned pine than in cottonwood forests, making the pine forests source populations and cottonwood stands sinks. Habitat-specific predation rates were responsible for consistency of productivity
between years in Eastern Kingbirds (Blancher and Robertson 1985, Murphy 2001),
European Jays (Andrén 1990) and Lewis’s Woodpeckers (Saab and Vierling 2001).

The inconsistent productivity I observed between sites suggests that no consistent
sources or sinks occur in this region, partly as a result of fluctuating predation rates.
Seasonal fecundity at KP was lower in 1998 than in 1999 and 2000 when the predation
rates were only about half of the 1998 level. The predation rate was highest at KP in
1998 then highest at WL in 1999 and 2000 when fecundity was lowest. This indicates
that predation rates were not related to differences in habitat at these sites but showed a
more random spatial and temporal pattern. Unlike Vander Haegen et al. (2002), I did not
find Brewer’s Sparrow nest predation rates to be consistently higher in smaller habitat
patches, although I did not study a wide range of patch sizes. Similarly, nest predation
was not consistently higher where sagebrush cover was lower. This spatial fluctuation in
predation rates would result if the dynamics of predator populations operated at larger
spatial scales or if predator cycles were unrelated to any recorded habitat differences
between the sites.

Few other studies have shown similar spatial shifts in productivity over time.
However, spatio-temporal interaction similar to that observed in this study has been
shown in Red-winged Blackbirds (Orians and Beletsky 1989) and House Sparrows
(Passer domesticus; Sæther et al. 1999, Ringsby et al. 2002). For Red-winged
Blackbirds, spatial fluctuations in nest predation were responsible for the pattern but for
House Sparrows, variation in clutch initiation related to weather was responsible.

The effects of a storm at different elevations also influenced site-related shifts in
productivity. While the high elevation sites lost nests in a storm, the same storm did not
affect nests at WL, the low elevation site. This advantage of low elevation at WL was not observed when breeding began later in 1999 and 2000. Due to its lower elevation, WL gets hotter and drier earlier in the season than do the higher elevation sites such that, when the onset of breeding is late, as it was in 1999 and 2000, the breeding season was actually shorter at WL leading to fewer nesting attempts. This was supported by the fact that fewer clutches were laid by WL females in 1999 and 2000 than in the earlier 1998 season.

These results showed that there was no best and worst site in terms of Brewer's Sparrow productivity. In order to maintain high regional productivity for Brewer's Sparrows at the northern edge of the range where conditions are unpredictable, sites must be protected from habitat loss or alteration across a range of elevations. This will allow for poor productivity at some sites to offset by high productivity at others as stochastic factors such as nest predation and weather conditions fluctuate.

It is possible that some of the spatio-temporal fluctuations in seasonal fecundity were generated by random factors resulting from the small sample sizes of females at each site in a particular year. Sample sizes of 9-15 females were used for the multiple spatio-temporal comparisons. With small sample sizes, it is possible that individual females that were particularly productive or unproductive could have led to lower precision of the mean seasonal fecundity estimate. Such small sample sizes may have reduced the power of individual site or year comparisons, thereby limiting my ability to detect differences between sites in a given year, or between years at a given site.
Seasonal Fecundity as a Measure of Productivity

Seasonal fecundity provided a more complete measure of productivity daily nest survival. Although daily nest survival was lower at SC in 1998 than in 2000, there was no corresponding difference in seasonal fecundity because females were able to compensate for early nest losses by making multiple nesting attempts. At KP daily nest survival did not differ between 1998 and 2000, although seasonal fecundity did, due to a higher number of clutches laid in 2000. Re-nesting and multiple brooding can account for significant portions of annual productivity. For example, House Martins (Delichon urbica) laid on average 1.7 clutches per year and fledged 1.49 clutches (Bryant 1989). Up to 87% of female Wood Thrushes in Ontario were double-brooded (Friesen et al. 2000) and double brooding accounted for increased productivity of Black-throated Blue Warblers in New Hampshire (Holmes et al. 1996). Most birds are capable of re-nesting and many of multiple brooding, so measuring the outcomes of all nesting attempts over the season is a more accurate estimate of productivity than simple nest success.

I demonstrated that the ability of a multiple-brooded species to achieve high seasonal fecundity was affected by its ability to trade-off the costs and benefits of early nesting when nest predation was stochastic in nature. However, longer-term data would be useful in determining how general these trade-offs are under changing environmental conditions. Brewer’s Sparrows breeding at the northern edge of their breeding range in British Columbia face environmental stochasticity associated with ENSO cycles and local, adverse weather events. During these weather fluctuations, site elevation played a role in their ability to maximize reproduction. In order to understand the role...
productivity plays in population dynamics, accurate measures of seasonal fecundity and an assessment of how it varies with environmental stochasticity are crucial.

LITERATURE CITED


CHAPTER 3:  

POPULATION VIABILITY OF BREWER'S SPARROWS AT THE NORTHERN EDGE OF THE RANGE

ABSTRACT

Breeding Bird Survey (BBS) data indicate that the Brewer's Sparrow has declined range-wide by 3% per year from 1966-2000, although there is geographical variation in the declining trend across the species' range. BBS data are insufficient to estimate a trend for British Columbia where the Brewer's Sparrow occurs at the northwestern edge of its breeding range. Peripheral populations may be more prone to extinction from environmental stochasticity than core populations due to greater scarcity of limiting resources and harsher environmental conditions. Here, I develop a stochastic, demographic population viability model to: (1) estimate the population growth rate ($\lambda$); (2) assess the importance of immigration from outside British Columbia to population stability; and (3) determine which vital rates most influence population growth.

The model predicts that the B.C. population of the Brewer's Sparrow will decline to extinction within 100 years without immigration. For the best-case scenario where mean adult survival was high (0.57) and years of low survival (0.26) occurred every 10 years, $\lambda = 0.93$. For the worst-case scenario where mean adult survival was lower (0.46) and low survival years occurred at random, $\lambda = 0.78$. Sensitivity analysis showed that the population growth rate was most sensitive to adult survival in both models, although the importance of fecundity increased in the best-case scenario. Given these results, management efforts for this species should focus on demographic connections between...
regions, particularly between source and sink breeding populations and explore the links between adult survival, the quality of non-breeding habitat and large-scale climatic fluctuations.

INTRODUCTION

Stochastic population models have become important tools in exploring factors related to population declines and in developing management strategies to halt those declines (Boyce 1992, Beissinger and Westphal 1998, Sjögren-Gulve and Ebenhard 2000, Beissinger and McCullough 2002, Morris and Doak 2002). Population viability analysis (PVA) models were developed to explore the roles that demographic and environmental stochasticity play in the persistence of small, endangered populations. Few, if any studies have specifically modelled the population dynamics of peripheral populations, which may be particularly affected by stochastic processes.

Peripheral populations may be more prone to decline through environmental stochasticity than larger, more stable populations in the range core (Maurer and Brown 1989, Lesica and Allendorf 1995, Garcia-Ramos and Kirkpatrick 1997). Random fluctuations in the size of any population can occur over time as a result of environmental stochasticity, the unpredictable changes in environmental conditions that affect mean population vital rates (May 1974, Shaffer 1981, Simberloff 1988, Lande 1993, 2002, Morris and Doak 2002). The effect of environmental stochasticity on population persistence depends upon population size and mean population growth rate (Lande 1993). Therefore, smaller, more variable populations at range edges that face limiting resources and environmental conditions are more vulnerable to decline over time (Caughley et al.)
Curnutt et al. (1996) showed that peripheral populations of nine grassland sparrow species were less abundant and more variable over time than were populations in the range core. They suggest that the persistence of such peripheral populations depends upon immigration from the core; however, little is known about the role that immigration plays in maintaining peripheral populations. Such source-sink dynamics between edge and core populations may buffer peripheral populations from the effects of greater environmental stochasticity (Pulliam 1988). However, if core populations decline, reducing the flow of immigrants, the peripheral population should decline more quickly. This was shown in a declining population of Florida Scrub Jays as recruits from peripheral areas moved into vacant core territories, hastening the decline at the periphery (Breininger 1999).

While the above evidence suggests that the conservation value of peripheral populations may be limited, recent evidence suggests otherwise. Channell and Lomolino (2000), and Rodriguez (2002) have shown that for a wide range of taxa, population declines were more severe in core than in peripheral areas of distributional ranges. This suggests that peripheral populations may be more resilient to population declines than previously thought, and more important to conservation when habitat loss is greater in the core versus the edges of the range.

Understanding the effects of individual demographic rates on population growth can elucidate the mechanisms driving population declines and focus conservation effort where it will have the biggest impact. One of the most useful roles for PVA in conservation biology is to identify, through sensitivity analysis, the vital rates that most influence model population trajectories (Reed et al. 1998, Mills and Lindberg 2002). For
migratory birds, it is particularly difficult to identify the effects and timing of limiting factors as constraints on reproduction and survival operate in distant geographical areas and diverse habitats. This has generated much recent debate about the relative contribution of limiting factors operating in summer, or winter or during migration (Sherry and Holmes 1995, Moore et al. 1995, Leu and Thompson 2002). While some studies find that population trends are most influenced by reproductive success (e.g., Sherry and Holmes 1992, Johnson and Geupel 1996, Siriwardena et al. 2000), others indicate that over-winter survival is most important (DeSante 1990). Recent evidence suggests that mortality during migration may be the strongest limiting factor for some species (Sillett and Holmes 2002).

I explored the dynamics of a peripheral population of a declining, grassland songbird, the Brewer's Sparrow, at the northern edge of its range in British Columbia. I estimated annual survival and dispersal of adults and juveniles and determined changes to breeding density at four sites from 1998-2000. I then built a stochastic demographic population viability model, incorporating the mean and variation of survival and fecundity rates. The objectives of the model were to estimate the population growth rate ($\lambda$) to evaluate population viability; to assess the importance of immigration from outside of British Columbia to population stability; and to determine which vital rates most influenced population growth.
METHODS

Annual Survival

I colour-banded breeding adults at four sites in the southern Okanagan and Similkameen Valleys, B.C. from 1997-2000 (see Chapter 2). I then estimated annual survival of adults from each site based on banding and re-sighting data using Program MARK (White 1999). Sequential models to test for the effects of year and site on survival estimates and re-capture rates were compared. First, the goodness of fit of the fully parameterized Cormack-Jolly-Seber (CJS) model \( \Phi_{\text{year} \times \text{site}} \cdot P_{\text{year} \times \text{site}} \) was assessed using a bootstrap method over 100 simulations to test that the assumptions of mark-recapture methods were met (Burnham et al. 1987, White 1999). The most parsimonious model with the smallest Aikake’s information criterion (AIC) was used to calculate survival estimates (Cooch and White 1998). Annual survival estimates were compared using program CONTRAST (Sauer and Williams 1989). Alpha levels for these multiple comparisons were determined using the Bonferroni adjustment \( \alpha = 0.05 / \# \text{ comparisons;} \) Neter et al. 1996). Estimates of male and female annual survival rates were calculated separately.

I colour-banded nestlings at age 4 – 5 days when they were large enough to band, but young enough to avoid premature fledging. The number of banded nestlings resighted in subsequent years was too low to support mark-recapture analysis.
Dispersal

Survival estimates are often biased by the loss of individuals that survive but disperse from the immediate study area (Koenig et al. 1996, Nathan 2001). Survival of juvenile migratory songbirds is particularly difficult to measure due to their high degree of natal dispersal (Greenwood and Harvey 1982, Anders et al. 1997). In an attempt to obtain better estimates of survival, particularly for juveniles, in 1998 I surveyed the areas around the study sites for banded individuals to a distance of approximately two kilometres. This also allowed for an assessment of breeding and natal dispersal between habitat patches in the region. This distance was chosen because it encompassed the areas between the three southern study sites and was feasible logistically. Observers walked along transects, 150 m apart and mapped all Brewer's Sparrows observed. Every 150 m, the observer stopped and recorded all individuals seen or heard for three minutes. Then a recorded Brewer's Sparrow song was played for three minutes and any additional birds observed were recorded. All individuals observed were followed until it could be determined if they were banded and all band combinations were recorded. In 1999 surveys were expanded to include four more sites within 50 km, where Brewer's Sparrow density was relatively high (Paczek 2002). Because these expanded surveys yielded no observations of dispersal, only the original 1998 transects were surveyed in 2000. Surveys were done once during the breeding season in 1998 and 2000 and twice in 1999.

Breeding Pair Density

To assess the population-level effects of variation in demography, the number of breeding pairs at each site from 1998 to 2000 was determined by mapping all territories.
Mapped territories included those held by: nesting, banded birds; by unbanded birds for which nests were found; by birds without an identified nest but which demonstrated breeding behaviour; and included areas with recently fledged young that did not belong to a known pair. Territories that overlapped site borders were counted if more than half of the territory occurred on the study site. Site boundaries were kept constant from year to year enabling me to track population changes at each site.

**Population Viability Analysis**

I developed a stochastic, single population viability model for Brewer's Sparrows in British Columbia. The objectives of developing the model were

i) to estimate the population growth rate ($\lambda$);

ii) to determine the importance of immigration to $\lambda$; and

iii) to determine which vital rate most strongly influenced $\lambda$.

As with most demographic models, parameters were modelled for females only (Noon and Sauer 1992) and all females were assumed to breed as one year-olds.

**Parameter Estimates**

*Population Size ($N$).* - The number of Brewer's Sparrows in British Columbia was estimated to be 400-500 breeding pairs in the early 1990s (Harvey 1992, Sarell and McGuinness 1996). However, these estimates were based on a one-time extensive survey of the region using roadside counts and widely spaced survey points. Such a survey conducted once in breeding season would greatly underestimate true regional population density, since it was restricted to roadsides and included no estimate of
detectability. To obtain a more accurate estimate, a double-sampling method was used. I compared density estimates from point counts done by S. Paczek in 1998 to density as determined by my breeding pair census method at the same sites. This ratio between the density of singing males at point counts to the density of known breeding pairs provided a correction factor for Harvey’s population estimates, assuming that densities have not changed greatly in the interim. The correction factor was remarkably consistent among sites ranging from 2.5 at WL to 2.9 at SC and averaging 2.63. Therefore a more robust estimate of the Brewer's Sparrow population in British Columbia is 1052-1315 (400-500*2.63) breeding pairs. I therefore used the mean number of 1184 breeding pairs as a starting population size to model population viability.

Fecundity (F).- Seasonal fecundity of females was estimated from 1998-2000 at four sites (see chapter 2). Data for all four sites were combined to estimate region-wide fecundity for each year. The mean and standard deviation (SD) of the number of fledglings per female across the three years was determined. I assumed that there was an even sex ratio among the fledglings, so to model females only, fecundity was halved.

Survival (S).- The mean and SD of adult female annual survival rates (S_a) as determined by mark-recapture analysis were used in the model. Juvenile survival was difficult to measure. Only a small portion of suitable habitat within the region was surveyed for dispersers. As well, surveys were done only once or twice a year, likely leaving many dispersers undetected. The fact that most dispersing juveniles were located at study sites (see Results), where intensive demographic work was done daily throughout the breeding season, rather than in surveyed areas, illustrates this point. Because I could not estimate juvenile survival without bias, I set it (S_j) to be half of that
of adult females in this model. Greenberg (1980) and Temple and Cary (1988) reviewed data on juvenile survival in migratory songbirds and showed that it is approximately half of adult survival. This value has been widely used in population modelling efforts (May and Robinson 1985, Howe et al. 1991, Thompson 1993, Donovan et al. 1995a, 1995b, Budnik et al. 2000).

Model Structure

A stage-based, stochastic model was developed in Excel (version 2000) based on the following growth equation:

\[ N_{t+1} = N_t(S_a + F S_j) \]  \hspace{1cm} (Eq. 3.1)

where \( N_t \) = number of adult females at the beginning of the breeding season in year \( t \), \( S_a \) = annual survival rate of adult females, \( F \) = number of female chicks fledged per adult female per year and \( S_j \) = survival rate of fledgling females to one year of age.

Variation in demographic rates mimics environmental stochasticity (Beissinger and Westphal 1998) and was included in the model by randomly sampling each year through the normal distribution of each vital rate, based on the mean and SD of each rate. I simulated population growth over 100 years and generated 1,000 replicate populations for each model run. The population growth rate \( (\lambda) \) was calculated for each year as \( N_{t+1}/N_t \). To better predict long-term population growth, the mean of log \( \lambda \) values over all simulations was determined (Morris and Doak 2002). Converting this value back to \( \lambda \), I assessed whether the model predicted the population to be stable \( (\lambda=1) \), increasing \( (\lambda>1) \), or deceasing \( (\lambda<1) \). Hereafter, this will be referred to as the base model.
There was considerable variation in adult survival rates over the three years of the study, the lowest being 0.26 (see Results). Most reviews of adult survival rates in migratory songbirds typically report rates between 0.40-0.60 (e.g. Cody 1971, Ricklefs 1973, Greenberg 1978). The few reported survival rates for North American migratory grassland birds range from 0.37-0.47 for Field Sparrow (Spizella pusilla, Carey et al. 1994), 0.35-0.50 for Grasshopper Sparrow (Ammodramus savannarum, Vickery 1996) to 0.53-0.63 for Nelson’s Sharp-tailed Sparrow (A. nelsoni, Post and Greenlaw 1982). Because my low survival rate (0.26) was considerably lower than these values, it may have been influenced by an irregular catastrophic mortality event. Therefore, I re-ran the model letting the mean survival rate vary randomly between the values for the other two years (0.47 - 0.66; mean = 0.57) and set adult survival to 0.26 every 10 years. The population growth rate was reassessed for this model. For comparison, the base model, with lower mean survival rate and low survival (0.26) occurring at random will be referred to as the worst-case scenario and the model with higher mean survival rate with low survival (0.26) occurring every 10 years will be referred to as the best-case scenario.

The importance of immigration to population viability was examined by assessing the number of immigrants needed each year for the population to be stable ($\lambda=1$). An immigration term was added to Eq. 3.1 for this run of the model such that:

$$N_{t+1} = N_t(S_a + FS_j) + I$$

(Eq.3.2)

where $I$ = the number of immigrant females (an equal number of male immigrants was assumed). $N_{t+1}$ was kept at 1184 so that the number of immigrants needed to maintain that population was

$$I = 1184 - (N_t(S_a + FS_j))$$

(Eq.3.3)
The mean number of immigrants and the mean percentage of the total population that was immigrants in any given year across all simulations were determined. The level of immigration necessary to maintain a stable population was calculated for both the best and worst case models.

Sensitivity analysis was used to explore the relative contributions of each vital rate to $\lambda$, for the best and worst case models. Each mean vital rate was changed by 5%, keeping all other rates the same while re-running the model.

RESULTS

Annual Survival

I colour-banded 272 adults; 132 were female and 140 were male. Goodness-of-fit testing showed that the data fit the Cormack-Jolly-Seber model, thereby meeting the assumptions of mark-recapture methods (female: $P = 0.37$; male: $P = 0.29$). The best model for both males and females showed that survival ($\Phi$) varied by year but not by site and that re-capture rate ($p$) was constant with respect to year and site ($\Phi_{year}, p$; Table 3.1). Annual survival was highest from 1997-1998, lowest from 1998-1999, and intermediate from 1999-2000 (Table 3.2). Female survival was significantly lower between 1998-1999 than between 1997-1998 ($X^2 = 5.84, P = 0.02, df = 1$; Table 3.2). Male survival was significantly lower between 1998-1999 than in the other two years (1997-1998: $X^2 = 10.79, P = 0.01, df = 1$; 1999-2000: $X^2 = 6.219, P = 0.01, df = 1$; Table 3.2).

Of 460 nestlings I colour-banded, only 24 were re-sighted (5.2%). Annual juvenile survival rates were 10% from 1997-1998, 5.9% from 1998-1999 and 3.4% from
1999-2000. As in adults, juvenile survival was highest from 1997-1998, but the lowest survival year for juveniles was 1999-2000, not 1998-1999 as in adults.

Table 3.1. Models for estimating survival for female and male Brewer’s Sparrows in the southern Okanagan and Similkameen Valleys, B.C., 1997 –2000. The five best models and the fully parameterized model are presented. (Φ = local survival, p = recapture rate; t = year and g = site AICc = Akaike’s information criterion and Deviance = model fit.)

<table>
<thead>
<tr>
<th>Model</th>
<th>AICc</th>
<th>ΔAIC</th>
<th>AIC Weight</th>
<th>Parameters in Model</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Φ(t) p(.)</td>
<td>214.71</td>
<td>0</td>
<td>0.59</td>
<td>4</td>
<td>26.99</td>
</tr>
<tr>
<td>Φ(t) p(t)</td>
<td>216.75</td>
<td>2.04</td>
<td>0.21</td>
<td>5</td>
<td>26.90</td>
</tr>
<tr>
<td>Φ(.) p(t)</td>
<td>218.92</td>
<td>4.21</td>
<td>0.07</td>
<td>4</td>
<td>31.20</td>
</tr>
<tr>
<td>Φ(.) p(.)</td>
<td>219.41</td>
<td>4.71</td>
<td>0.06</td>
<td>2</td>
<td>35.87</td>
</tr>
<tr>
<td>Φ(t) p(g)</td>
<td>220.18</td>
<td>5.47</td>
<td>0.04</td>
<td>7</td>
<td>25.97</td>
</tr>
<tr>
<td>Φ(g<em>t) p(g</em>t)</td>
<td>232.55</td>
<td>17.84</td>
<td>0.00</td>
<td>18</td>
<td>12.17</td>
</tr>
<tr>
<td>Male</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Φ(t) p(.)</td>
<td>264.702</td>
<td>0</td>
<td>0.58</td>
<td>4</td>
<td>24.01</td>
</tr>
<tr>
<td>Φ(t) p(t)</td>
<td>265.860</td>
<td>1.16</td>
<td>0.32</td>
<td>5</td>
<td>23.06</td>
</tr>
<tr>
<td>Φ(t) p(g)</td>
<td>268.957</td>
<td>4.26</td>
<td>0.07</td>
<td>7</td>
<td>21.87</td>
</tr>
<tr>
<td>Φ(.) p(t)</td>
<td>272.969</td>
<td>8.27</td>
<td>0.01</td>
<td>4</td>
<td>32.28</td>
</tr>
<tr>
<td>Φ(.) p(.)</td>
<td>273.254</td>
<td>8.55</td>
<td>0.01</td>
<td>2</td>
<td>36.71</td>
</tr>
<tr>
<td>Φ(g<em>t) p(g</em>t)</td>
<td>287.024</td>
<td>22.32</td>
<td>0.00</td>
<td>18</td>
<td>14.57</td>
</tr>
</tbody>
</table>

Table 3.2. Annual survival estimates (% of birds banded that survived) and their standard errors of adult Brewer’s Sparrows in the southern Okanagan and Similkameen Valleys, B.C., 1997 –2000 (different letters indicate significant comparisons between years; female = upper case, male = lower case). S.E. = standard error, N = sample size.

<table>
<thead>
<tr>
<th>Year</th>
<th>N</th>
<th>Annual Survival Estimate (Φ)</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997-1998&lt;sup&gt;a&lt;/sup&gt;</td>
<td>45</td>
<td>female 0.66</td>
<td>0.16</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>male 0.60</td>
<td>0.08</td>
</tr>
<tr>
<td>1998-1999&lt;sup&gt;b&lt;/sup&gt;</td>
<td>63</td>
<td>female 0.26</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td>45</td>
<td>male 0.29</td>
<td>0.05</td>
</tr>
<tr>
<td>1999-2000&lt;sup&gt;a&lt;/sup&gt;</td>
<td>31</td>
<td>female 0.47</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>54</td>
<td>male 0.51</td>
<td>0.07</td>
</tr>
</tbody>
</table>
Dispersal

Adults in this population showed a high degree of breeding site philopatry. Only one case of breeding dispersal, the movement of an adult from one breeding site to another in a subsequent year, was observed. A female who bred at SC in 1999 became a breeder at IG in 2000, moving over 4 km between seasons. Five adult females (3.8%) and two males (1.4%) moved just outside the site boundaries between seasons, moving less than 1 km between years. Individual study sites were linked by natal dispersal, the movement of juveniles from natal sites to other sites where they became breeders. Seventeen percent of re-sighted chicks demonstrated natal dispersal. One male from KP became a breeder at IG ~ 8 km away. One male from SC bred at IG ~ 4 km away and another became a breeder 40 km away at WL. A male from IG bred at KP ~ 8 km away.

Breeding Pair Density

Across years, the combined population size at the four sites decreased from 168 pairs in 1998 to 155 pairs in 1999 to 139 pairs in 2000, a mean decrease of 9%/year (Fig. 3.1). The population trends over three years differed between the sites. KP showed the most stable population trend with 44 pairs in 1998, 43 in 1999, then increasing to 49 pairs in 2000 (Fig. 3.1). The population at SC decreased from 40 to 29 between 1998 and 1999, decreasing by 2 further pairs in 2000 (Fig. 3.1). At IG, the number of pairs initially
increased from 33 in 1998 to 41 in 1999 then declined to 35 in 2000 (Fig. 3.1). The WL population declined steadily from 51 pairs in 1998 to 42 in 1999 to 28 in 2000 (Fig. 3.1).

**Figure 3.1.** Trends in abundance of Brewer Sparrow breeding pairs at four sites in the southern Okanagan and Similkameen Valleys, B.C. 1998-2000.

Population Viability Analysis

*Parameter Estimates.*- The mean number of chicks per female (fecundity) used in the models was $3.05 \pm 0.61$. Mean adult survival was $0.46 \pm 0.20$ for the worst-case scenario and $0.57 \pm 0.13$ for the best-case scenario. Juvenile survival was modelled as $0.5 *$ adult survival.

*Population Growth Rate ($\lambda$).*- The mean $\lambda$ value for 1,000 simulations of the worst-case model was 0.78, indicating a rapidly declining population. The population
declined by a mean of 18.9% per year. All populations went extinct by within 59 years and the mean time to extinction was 28.4 years (SD 6.96) (Fig 3.2).

Fig. 3.2. Mean population trajectories from 1000 simulations of stochastic population models for Brewer's Sparrows in British Columbia. Models do not include immigration.

The best-case model showed a slower, but steady population decline with a mean $\lambda$ of 0.93 over 100 years, declining on average by 4.7%/year (Fig 3.2). Sixty-three percent of the 1,000 simulated best-case populations went extinct within 100 years with a mean extinction time of 87.1 years (SD 10.1).

Immigration.- On average, 378 breeding pairs would have to immigrate into the B.C. population each year for the Brewer's Sparrow population to be stable over time (mean $\lambda$=1, worst-case model). This means that, on average, 22% of the breeding adults would be immigrants in any given year. Even when low survival occurred at ten-year intervals and mean adult survival was higher, 126 pairs, or 10.6% of the breeding
population would have to be immigrants each year to keep the population stable (best-case model). This suggests that continued immigration from further southern in the range is essential for population viability.

*Sensitivity Analysis.* Adult survival was the vital rate that most influenced population growth in the worst-case model, followed by juvenile survival and fecundity (Table 3.3).

### Table 3.3. Sensitivity of the mean population growth rate of 1,000 simulated populations of Brewer’s Sparrows in British Columbia to increases of 5% in the value of model vital rates.

<table>
<thead>
<tr>
<th>Vital Rate</th>
<th>% Change in $\lambda$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Worst-case Model</strong></td>
<td></td>
</tr>
<tr>
<td>Adult annual survival</td>
<td>3.30</td>
</tr>
<tr>
<td>Juvenile annual survival</td>
<td>1.72</td>
</tr>
<tr>
<td>Seasonal fecundity</td>
<td>1.16</td>
</tr>
<tr>
<td><strong>Best-case Model</strong></td>
<td></td>
</tr>
<tr>
<td>Adult annual survival</td>
<td>5.40</td>
</tr>
<tr>
<td>Seasonal fecundity</td>
<td>4.94</td>
</tr>
<tr>
<td>Juvenile annual survival</td>
<td>2.12</td>
</tr>
</tbody>
</table>

Adult survival was also the most influential vital rate in the best-case model, but only marginally better than fecundity (Table 3.3). Both were more important than juvenile survival (Table 3.3). Both increases and decreases of 5% in vital rates showed the same pattern of relative importance of vital rates, so only the increases are shown. This result indicates that the viability of Brewer’s Sparrows in British Columbia is limited by factors acting on adult survival and operating away from breeding grounds, either during migration or in the southern US or Mexico during the non-breeding season. However, productivity is almost as influential as survival in the best-case model.
suggesting that high productivity is important in overcoming relatively rare survival catastrophes.

**DISCUSSION**

**Population Viability and Immigration**

Population viability analysis of the Brewer's Sparrows in British Columbia suggests that this northern, peripheral population cannot be sustained without immigration from more southern populations. This supports the Curnutt *et al*. (1996) scenario where highly variable edge populations of grassland sparrows are maintained by immigration from more stable, core areas. In this case, immigration from stable, nearby Washington populations, rather than from distant core areas may support the B.C. Brewer's Sparrow population. Demographic rescue by immigration was shown to be crucial for the persistence of small, isolated populations of the Acorn Woodpecker (*Melanerpes formicivorus*; Stacey and Taper 1992). Breeding Bird Survey data suggest that Brewer's Sparrows have declined across their range at 3%/year from 1996-2000 (Sauer *et al*. 2001). My models predict annual declines of 18.9% for the worst-case scenario, and 4.7% for the best-case scenario for the B.C. population, both steeper declines than the range-wide average. This pattern of faster peripheral declines would be expected if the core decline reduced the immigrant pool necessary to maintain peripheral populations. Although Rodriguez (2002) found that declines in many bird species were concentrated in high abundance core areas, range contraction, or the loss of peripheral populations was also occurring. This suggests that the loss of immigrants from declining
core areas may eventually lead to peripheral extirpations. Faster peripheral declines would also be expected if first-year recruits from B.C. are drawn into empty territories resulting from declines in core regions, a pattern observed in a declining Florida Scrub Jay population (Breininger 1999).

The range-wide Brewer's Sparrow decline is not spatially consistent. Populations in core areas such as Idaho and Oregon have declined significantly (5.2% and 2.5% per year respectively), whereas peripheral populations in New Mexico and Washington appear stable (Sauer et al. 2001). The stability of the nearby Washington population may provide a sufficient flow of immigrants to keep the B.C. population from declining over time. Movement of Brewer's Sparrows between Washington and British Columbia is likely frequent since the breeding range is contiguous along a 15 km stretch of the Canada-US border. The breeding range in B.C. forms a narrow, northward projection of a wider distribution that covers the Columbia Basin of eastern Washington (Rotenberry et al. 1999). My study showed that Brewer's Sparrow adults are highly philopatric, but dispersing first-year birds moved up 40 km. Therefore, natal dispersal of first-year birds between B.C. and Washington is probable. In agreement with this scenario of frequent movements, a recent study by Croteau (2002) revealed moderate to high levels of gene flow in Brewer's Sparrows between my four sites, three other sites in the region and one in central Washington, although there was a small degree of genetic differentiation among sites. The low degree of natal philopatry and high degree of adult philopatry I observed suggests mechanisms for these genetic patterns and demonstrate the role that immigration plays in Brewer's Sparrow demography at a larger scale.
BBS data provide insufficient coverage to assess the long-term population trend for the Brewer's Sparrow in British Columbia and as no other long-term data exist, it is impossible to validate the predictions of my PVA models at this time. The trend estimate from four sites in the region shows an average 9%/year decline; however, this average was strongly weighted by a steep decline at one particular site, WL and such short-term trends are unlikely to be predictive of long-term trends. Therefore, the model trend predictions provide hypotheses about the population trend in B.C., which can only be tested by initiating a long-term monitoring program for this species of increasing conservation concern.

Variation in Demographic Rates

I used parameter estimates generated from three years of field data, encompassing the strong El Niño and La Niña events of 1997-1998 and 1998-1999, respectively (Environment Canada 2002). By capturing the shift in environmental conditions between the El Niño and La Niña years, I measured a greater range of vital rates than would have occurred in a normal 3-year period. While the use of short-term datasets to measure demographic parameters tends to underestimate variance in vital rates and the occurrence of catastrophic events, the large range in the vital rates I measured may have compensated for the short duration of the sampling period (Pimm and Redfern 1988, Arnio and Pimm 1995, Beissinger and Westphal 1998, Ludwig 1999, Beissinger 2002).

Productivity and survival of birds are related to large-scale climatic patterns including ENSO (El Niño Southern Oscillation) and NAO (Northern Atlantic Oscillation)
(Forchhammer et al. 1998, Sæther et al. 2000, Sillet et al. 2000, Both and Visser 2001, Nott et al. 2002). Productivity of Brewer's Sparrows was lowest in 1998, the El Niño year, intermediate in 1999, the La Niña year, and highest in 2000. Adult female survival was highest in 1997-1998, the El Niño year, lowest in the La Niña year, 1998-1999) and intermediate in 1999-2000. While this suggests that large-scale weather patterns play a role in the demography of this population, measurement of vital rates over more ENSO cycles is necessary to determine how closely demographic rates are tied to large-scale climatic oscillations.

Wet conditions in El Niño years have been linked to increases in food supply and higher bird productivity in western North America. Nott et al. (2002) found that productivity of neotropical migrants wintering in western Mexico and breeding in the Pacific Northwest was higher in summers following an El Niño winter. Similarly, Morrison and Bolger (2002) found that Rufous-crowned Sparrow productivity was highest in an El Niño year and lowest in the following La Niña year. Productivity and survival of Black-throated Blue Warblers breeding in the eastern US and wintering in Jamaica, where conditions are drier in El Niño years, were both lower in El Niño years and higher in La Niña years (Sillet et al. 2000).

Contrary to these findings, productivity in this study was lowest in the spring following the El Niño winter (1998). Although Brewer's Sparrows initiated breeding early that year, a late May storm killed chicks of most first clutches at two of four sites (see Chapter 2). Higher survival over the El Niño winter and lowest survival over the La Niña winter, supports the hypothesis that rainfall enhances food during wet periods while food is limited during dry ones (Dunning and Brown 1982). Precipitation in the
southwestern US and Mexico, where Brewer's Sparrow winter, was lower in La Niña years (Null and Monteverdi 1999). However, longer-term demographic data are necessary to determine the cause-effect linkages between ENSO cycles and Brewer’s Sparrow demography.

**Sensitivity Analysis**

Sensitivity analysis demonstrated the importance of adult survival to population growth of Brewer's Sparrow in B.C. Outcomes of two scenarios that were generated by changing the frequency of low adult survival years illustrate how variation in survival affects the models. The worst-case model population declined almost four times faster than the best-case model, which had a higher mean survival value and low survival occurred every ten years. However, even a mean survival rate of 57% of adults in nine years out of ten was not high enough to overcome steep population declines after catastrophic years. If low survival is closely linked to dry winter conditions during La Niña years, a catastrophic year only once a decade may be overly optimistic. El Niño and La Niña conditions vary in intensity and occur on average every 2-7 years (NAOO 2002). Current evidence suggests that ENSO events are becoming more frequent and persistent with increased global temperatures (IPCC 2001). An increasing frequency of low survival years will lead to quicker population declines without compensatory immigration (Martin et al. 2000).

If population viability of Brewer's Sparrows in B.C. was most sensitive to changes in adult survival in non-breeding areas, then conservation efforts focused on improving the amount and quality of breeding habitat alone will be unsuccessful in
maintaining this population. Adult survival varied between the years of the study but not between the breeding sites. Efforts to secure and enhance non-breeding habitat in the southwestern US and central Mexico should be a principal focus of any conservation plan. Most research and conservation planning for North American migratory songbirds is biased in favour of habitat management on breeding grounds (Hutto 1985, Sherry and Holmes 1995, Petit et al. 1995). The quantity and quality of migration stop-over sites may also influence survival in migratory birds (Moore et al. 1995, Leu and Thompson 2002). In fact, mortality may be highest during the migration phase of the annual cycle (Sillett and Holmes 2002). Those mortality risks may be higher for individuals in northern peripheral breeding populations because they probably have to travel further between wintering and breeding habitat. It is not known if Brewer's Sparrows breeding in B.C. face higher mortality risks during migration, because the distribution of breeding populations in wintering areas is not known.

When survival was higher in the best-case scenario model, the influence of productivity on population trajectory was enhanced. This suggests that if I underestimated the survival rate, I may have overestimated its importance to driving population dynamics. Therefore, maintaining high quality breeding habitat in British Columbia may be as essential to population persistence as non-breeding habitat conservation. This may be especially true if habitat enhancement to increase productivity is easier to accomplish than affecting change in factors related to survival, as survival may be driven more by weather-related phenomenon.

Sensitivity analysis can also point out the importance of uncertainty in demographic parameter estimates for predictions of population viability, which can assist
in the design of research and monitoring programs (Beissinger and Westphal 1998,
Burgman 2000, Morris and Doak 2002). Uncertainty in adult survival is most likely to
bias the model predictions in this study. Therefore, future monitoring efforts should
focus on obtaining better long-term estimates of variation in survival rates to determine
how often extreme low survival rates occur. The models assume that adults that did not
return were lost to the B.C. population, either through mortality or permanent emigration.
Because I observed such a high degree of breeding-site fidelity between years in adults,
this is likely true and emigration was assumed to be negligible. However, if some
breeders moved to areas that I didn’t survey, survival rates may have been
underestimated and represent local minimum survival estimates. Such a bias in the adult
survival rate would have resulted in an underestimate of the population growth rate. The
assumption that juvenile survival was half of adult survival is more uncertain, but in light
of the difficulty in obtaining better field estimates, it is a best guess. If juvenile survival
was actually higher, the model may have underestimated both the population viability
and the importance of this vital rate.

A similar bias in measuring seasonal fecundity may have resulted if all successful
nesting attempts by females were not discovered, leading to underestimates of the
number of chicks fledged. This may have happened if females moved to another territory
after initial breeding attempts, especially if these new territories were off the study site.
One such case was observed at WL when a female whose first attempt failed was
discovered later in the season, during a survey, at a nest off the study site. Such
underestimates of fecundity could lead to overly pessimistic model-derived population
growth rates.
While biases in demographic rate estimates may have resulted in overly pessimistic results, the lack of density dependence in the models may have had the opposite effect. When density dependence is not considered in PVA models, extinction rates tend to be underestimated (Morris and Doak 2002, Beissinger and Westphal 1998). Most PVA models include density dependence by including a ceiling on the population size beyond which the population can’t grow. An earlier version of my models included such as ceiling, but since the population trends were consistently downwards, the ceiling was rarely reached. Therefore, the absence of density dependence may have not affected the model outcomes in this study. However, building density dependence into demographic rates can result in less pessimistic model outcomes than models using a density-dependent population ceiling (Brook and Kikkawa 1998, McCallum et al. 2000). Although this approach may be more realistic, most studies, including this one, lack the long-term data necessary to determine density dependent responses of individual vital rates.

Conservation Implications

The most useful roles for PVA in conservation planning are in developing testable hypotheses about causes of population declines, comparing the relative effects of different management strategies on population persistence and developing appropriate research and monitoring strategies (Beissinger and Westphal 1998, Burgman 2000, Beissinger 2002, Morris and Doak 2002, Reed et al. 2002). The results of this PVA lead to the hypotheses that the Brewer's Sparrow population in B.C. is not viable over 100 years without immigration and that adult survival is most limiting to population growth.
The conservation implications of this study are clear. Conservation planning based solely on political boundaries and focused only on breeding season habitat management could fail to sustain this population in B.C. Determining the causes and rates of mortality in non-breeding habitat may be as important as improving breeding habitat quality.

An appropriate research and monitoring strategy for Brewer's Sparrows would:

1) establish long-term monitoring to test whether the population is declining as the model predicts;
2) improve the accuracy of fecundity and survival estimates by measuring them over more seasons;
3) target research to determine the rates and causes of mortality in winter and at migratory stopover habitats; and
4) relate geographical differences in population trends throughout the species’ range to variation in fecundity and survival.

Because of the short-term nature of the field data used to estimate demographic parameters here, the value of my models is principally to generate hypotheses about what limits the Brewer's Sparrow population in B.C. They are not yet an accurate prediction of the ultimate fate of this population. The research and monitoring strategy I suggest would provide information for further model refinement and lead to better population predictions.
LITERATURE CITED


Chapter 4:

Nest-Site Selection in Relation to Nest Success in Brewer’s Sparrows

ABSTRACT

Nest site selection can have important fitness consequences for birds. I tested the hypothesis that Brewer’s Sparrows selected nesting habitat to reduce the risk of predation at four sites in the southern Okanagan and Similkameen Valleys, British Columbia. First, I examined nest-site selection at the levels of the nest shrub and the 5-m radius nest patch by comparing habitat variables at nest sites to those at non-nest sites. I then compared the same variables between successful and depredated nests. Brewer’s Sparrows selected nest shrubs that were taller, thinner and more concealed from the south at one site and shrubs that were more concealed from overhead and from the north and south sides at the other sites. At the nest patch level, shrub cover was consistently greater at nest patches than at non-nest patches. These results suggest that nest-site selection operates to conceal nests. However, the habitat variables related to concealment did not differ strongly between successful and depredated nests. The nest sites that Brewer’s Sparrows choose may not be the most successful because predation risk varies at larger spatial scales, and because predators with differing search strategies cover all the possible safe havens available.

INTRODUCTION

The non-random use of habitats by organisms is thought to be a consequence of natural selection (Southwood, 1977, Cody 1985, Martin 1998). For open-cup nesting
bird species, the predation of nests is the dominant factor limiting productivity, although other factors such as food limitation and thermal conditions may also play a role (Nice 1957, Ricklefs 1969, Martin 1995). The nest concealment hypothesis suggests that predation pressure leads to a preference for nest-sites that conceal nests from potential predators (Martin 1992, Martin 1998, Clark and Shutler 1999). Vegetation immediately surrounding the nest may conceal visual, olfactory and auditory clues from predators (Martin 1992, Burhans and Thompson 1998). Vegetation in the patch around the nest may obscure the movements of adults to and from the nest. As well, dense vegetation might increase a predator’s search effort, reducing its efficiency, as it must explore many more potential nest sites (Bowman and Harris 1980, Martin and Roper 1988, Filliater et al. 1994). However, vegetation surrounding the nest may obscure the view of incubating birds, increasing their vulnerability to predation. Nest-site selection may therefore be a trade-off between egg/chick survival and adult vulnerability (Götmark et al. 1995, Wiebe and Martin 1998).

Many studies have examined nest-site selection in birds and have identified habitat characteristics that are selected preferentially, i.e. used more often than generally available in the environment (e.g. Martin and Roper 1988, Clark and Shutler 1999, Ford 1999, McLeod et al. 2000, Bowman and Woolfenden 2002). Most recent studies have examined whether these preferred habitats do indeed lead to reduced predation rates, and the evidence has been equivocal. For example, preferred habitats were associated with reduced predation rates in some prairie ducks (Clark and Shutler 1999), Hermit Thrushes (*Catharsus guttatus*; Martin and Roper 1988), Inca Terns (*Larostrens inca*; Velano and Márquez 2002), Black Woodpeckers (*Dryocopus martinus*; Rolstad et al. 2000) and
Lesser Kestrels (*Falco naumanni*; Negro and Hidalgo 1993). However, preferred habitat characteristics were not associated with reduced predation in species such as Song Sparrows (*Melospiza melodia*; Chase 2002), Dusky Flycatchers (*Empidonax oberholseri*; Liebezeit and George 2002), Yellow-breasted Chats (*Icteria virens*; Ricketts and Ritchison 2000), Noisy Friarbirds (*Philemon corniculatus*; Ford 1999) and Hooded Warblers (*Wilsonia citrina*; Whittam et al. 2002). Clearly, more information on the relationship between nest-site selection and nesting success is needed. Questions remain about the scales at which nest-site selection and nesting success are connected and about how predators use habitat types at these scales. Answers to these questions will help land managers and conservation biologists concerned with managing for species of concern by identifying habitat features that are not only preferred, but that lead to greater productivity.

Brewer's Sparrows are declining across their breeding range in shrub-steppe habitats of western North America (Sauer et al. 2001). Identifying habitat components related to productivity will allow better management of impacts such as livestock grazing, fire control and invasive weeds. I examined nest-site selection in Brewer's Sparrows in the Okanagan and Similkameen Valleys, B.C. in 1998 and 2000. As expected, nest predation was the major cause of nest failure in this population (see Chapter 2). I tested the hypothesis that nest-site characteristics were associated with nest success. In particular, I hypothesized that the use of dense vegetation reduced the risk of predation. To address this hypothesis, I first asked whether Brewer's Sparrows showed habitat preferences at the scale of the nest shrub and the 5-m radius patch around the nest. I then asked whether preferred habitat variables were linked to lower predation rates.
METHODS

Study Sites and Nests

Nests were located throughout the breeding season at four sites from 1997 to 2000 (see chapter 2). At each site in 1998, 15 successful (fledging at least one chick) and 15 depredated nests were chosen for analysis of nest-site selection. Only one nest per female was included in each year’s sample. Nesting habitat was not assessed in 1999. As there were fewer nests overall in 2000 and more were successful, there were only enough nests for equal samples of successful and depredated nests at White Lake and Kilpoola. Ten successful and ten depredated nests were chosen at these sites in 2000.

I examined local nest-site selection by comparing used nest sites to available nesting habitat within territories. Available habitat was sampled by choosing a point at a random direction and distance up to 100m from each nest. Directions and distances were divided in 10° or 10 m increments and were drawn at random, with drawn values replaced after each draw. Although territory boundaries were not determined, Brewer’s Sparrow territories range from 0.55 to 2.36 ha (Rotenberry et al 1999), so a point less than 100 m from the nest would likely be in the same territory. The nearest shrub (of the same species as the nest shrub) to the random point was used for comparison to the nest. Only shrubs large enough to support a Brewer’s Sparrow nest were used. To test whether preferred habitat variables were associated with greater nest success, I then compared the same habitat variables at successful versus depredated nests.
Habitat Variables

I measured habitat variables at two scales, the nest shrub and the 5m-radius patch surrounding the nest. The variables measured were a subset of those suggested by the BBIRD field protocol (Martin et al. 1997). Nest shrub variables measured included: height, width and aspect (Table 4.1). The position of the nest within the shrub was assessed by measuring: the distance from bottom of the nest to the ground, the distance from the centre of the nest to the centre of the shrub, the distance from the centre of the nest to the nearest edge of the shrub, and the orientation of the nest in relation to the centre of the shrub (Table 4.1). As a measure of nest concealment from above, the percentage of the nest obscured from directly above the shrub was estimated. The percentage of the nest concealed from the sides was estimated by observing the nest from the sides, 1 m from the shrub in the four cardinal directions (Table 4.1). These measurements, except those for nest position, were also taken at non-nest shrubs. To estimate concealment at non-nest shrubs, a cloth the colour of the dried grasses that compose Brewer's Sparrow nests was rolled into a ball the approximate size of a nest and placed near the centre of the non-nest shrub. While this placement was somewhat arbitrary, most Brewer's Sparrow nests were found near the centre of shrubs and I considered it a good approximation for concealment of a possible nest.

I measured fifty patch-level habitat variables at nest and non-nest patches. This number was reduced to 14 by combining categories and by removing highly correlated variables (correlation coefficient >0.7, Tabachnick and Fidell 2001). Ground cover was characterized by dividing the 5-m radius patch into four sections. I scored the percentages of the ground covered by cryptogamic crust, rock, litter, bare ground, grass,
forbs and shrubs under 25 cm tall in each section. The percentages from the four sections were averaged (Table 4.2).

Table 4.1. Shrub-level variables measured at Brewer’s Sparrow nest shrubs and non-nest shrubs.

<table>
<thead>
<tr>
<th>Shrub-Level Variables</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrbht</td>
<td>Height of nest or non-nest shrub</td>
</tr>
<tr>
<td>Shrbwd</td>
<td>Width of nest or non-nest shrub</td>
</tr>
<tr>
<td>Nstht</td>
<td>Height of nest from ground</td>
</tr>
<tr>
<td>Dstcntr</td>
<td>Distance of nest to centre of shrub</td>
</tr>
<tr>
<td>Dstedg</td>
<td>Distance of nest to nearest edge of shrub</td>
</tr>
<tr>
<td>Orient</td>
<td>Orientation of nest with respect to shrub centre</td>
</tr>
<tr>
<td>Aspect</td>
<td>Aspect of ground at nest shrub</td>
</tr>
<tr>
<td>ConcealO</td>
<td>% nest concealed from overhead</td>
</tr>
<tr>
<td>ConcealN</td>
<td>% nest concealed from north</td>
</tr>
<tr>
<td>ConcealS</td>
<td>% nest concealed from south</td>
</tr>
<tr>
<td>ConcealW</td>
<td>% nest concealed from west</td>
</tr>
<tr>
<td>ConcealE</td>
<td>% nest concealed from east</td>
</tr>
</tbody>
</table>

The composition of the shrub layer was characterized similarly. The percentages of the most common shrub species, Big Sagebrush (*Artemisia tridentata*), Giant Wildrye (*Leymus cinereus*), Common Snowberry (*Symphoricarpos albus*), Common Rabbitbrush (*Ericameria nauseosus*) and Threetip Sagebrush (*Artemisia tripartita*), were estimated in each section of the patch and averaged across sections (Table 4.2). Shrubs of other species were grouped into the category Other. Although Giant Wildrye is a grass, it was categorized as a shrub since it can grow to 70-220 cm (Douglas et al. 2001) and was used by Brewer's Sparrows for nesting and perching. The height of herbaceous growth was
measured at the nest or focal shrub and at one, three and five metres from the nest in the four cardinal directions, and all measures were averaged (Table 4.2).

**Table 4.2.** Patch-level variables measured at Brewer's Sparrow nest patches and non-nest patches.

<table>
<thead>
<tr>
<th>Patch Level Variables</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crust</td>
<td>% of ground covered in crust</td>
</tr>
<tr>
<td>Rock</td>
<td>% of ground covered rock</td>
</tr>
<tr>
<td>Litter</td>
<td>% of ground covered in litter</td>
</tr>
<tr>
<td>Bare</td>
<td>% of ground bare</td>
</tr>
<tr>
<td>Grass</td>
<td>% of ground covered in grass</td>
</tr>
<tr>
<td>Forb</td>
<td>% of ground covered in forb</td>
</tr>
<tr>
<td>SmShrub</td>
<td>% of ground covered in shrubs&lt;25 cm tall</td>
</tr>
<tr>
<td>HrbHt</td>
<td>average herbaceous height (cm)</td>
</tr>
<tr>
<td>BigSage</td>
<td>% shrub layer in Big Sagebrush</td>
</tr>
<tr>
<td>Rye</td>
<td>% of shrub layer in Giant Wildrye</td>
</tr>
<tr>
<td>Snowberry</td>
<td>% of shrub cover in Snowberry</td>
</tr>
<tr>
<td>Rabbitbrush</td>
<td>% of shrub layer in Rabbitbrush</td>
</tr>
<tr>
<td>3-TipSage</td>
<td>% of shrub layer in 3-tip Sagebrush</td>
</tr>
<tr>
<td>Other</td>
<td>% of shrub layer in other shrub species</td>
</tr>
<tr>
<td>TotalShrub</td>
<td>% of shrub layer in shrubs of all species</td>
</tr>
</tbody>
</table>

**Statistical Analyses**

All percentage data were arcsine-square-root transformed. Aspect and orientation data were transformed using a formula for circular data \( V = \cos (A-45) + 1 \); Beers *et al.* 1966). Univariate comparisons of each variable were used to determine if there were differences between the sites, and for WL and KP, if there were differences between years. These comparisons were performed for nest shrubs and patches and non-nest shrubs and patches separately.

I used multiple logistic regression models to compare habitat between nest and non-nest shrubs and patches and between shrubs and patches with successful and
depredated nests. This method was chosen because many of the variables were not normally distributed and logistic regression makes no assumptions about the distribution of predictor variables (Tabachnick and Fidell 2001). I used stepwise logistic regression with Wald Chi-square statistics to decide which variables to retain; variables entered the model if \( p < 0.15 \) and were removed if \( p > 0.20 \). Hosmer and Lemeshow (2000) suggest using these less stringent \( P \)-values to avoid removing from the model variables that are significantly related to the dependent variable. Hosmer and Lemeshow goodness-of-fit tests were used to assess how well the models fit the data (Hosmer and Lemeshow 2000).

The logistic regression models were re-run with the sum of the percentages of the individual species to test whether total shrub cover, regardless of species composition was a better predictor. These models were compared to the original ones using Aikake's Information Criteria (\( \text{AIC}_c \)) to see which model best fit the data (Burnham and Anderson 1998). Statistical analyses were conducted using SAS version 8 (SAS Institute 2002) and SPSS version 11.0 (SPSS Inc. 2002).

RESULTS

Nest Shrub

Shrub height was the only shrub variable that differed between years of the study. It was higher in nest shrubs at WL in 2000 vs. 1998 (\( P = 0.002 \)) and was higher in non-nest shrubs at both sites in 2000 than in 1998 (KP: \( P = 0.012 \); WL: \( P = 0.012 \)). These differences reflect the growth of the shrubs over the two years. Because all other variables did not differ, data from 1998 and 2000 were pooled.
Almost all differences of shrub variables between sites occurred between SC and one or more other sites. Nest shrubs were wider at IG \((P = 0.005)\) and WL \((P = 0.013)\) than at SC, though also wider at IG than KP \((P = 0.044)\).Dstcntr was greater at WL than at SC \((P = 0.033)\). ConcealS was higher at SC nest shrubs than at the other sites \((P = 0.014)\). When SC nest shrubs were compared to all other sites as a group, they had smaller values for Shrbht \((P = 0.047)\), Shrbwd \((P = 0.006)\), Nstht \((P = 0.028)\), Dstcntr \((P = 0.002)\), and Dstedg \((P = 0.05)\). Comparison between sites for non-nest shrubs also showed SC differing from other sites with lower Shrbht than at KP \((P = 0.043)\) and than all other sites combined \((P = 0.05)\). ConcealW was greater at SC than at the other sites \((P = 0.034)\) and Aspect was lower (closer to southwest; \((P = 0.014)\).

These differences between SC and the other sites reflect the fire that removed much of the shrub cover from SC in 1994 (see Chapter 1). Brewer's Sparrows at SC generally have smaller shrubs available for nesting and, as there was less overall shrub cover at the site, they nested in a wider variety of shrubs and smaller plants. For this reason all analyses at the shrub level were done separately for SC while the rest of the sites were grouped together.

Nest shrubs at SC were taller, thinner and had more cover on the south side than did non-nest shrubs (Table 4.3). At the other sites, nest concealment was greater from overhead and from the north and south than at non-nest shrubs (Table 4.3).

Successful nests at SC were closer to the centre of shrubs and were more concealed from the east than were depredated ones (Table 4.4). Shrubs with successful nests tended to be on south or southwest facing slopes and those with depredated nests on more northerly facing slopes (Table 4.4). At the other sites, successful nests were higher
in shrubs and were more concealed from the north than were depredated ones (Table 4.4).

They were however less concealed from overhead and from the west than were depredated nests (Table 4.4).

**Table 4.3.** Significant shrub-level predictors of Brewer's Sparrow nest-site selection as determined by logistic regression.

<table>
<thead>
<tr>
<th></th>
<th>Wald $X^2$</th>
<th>df</th>
<th>P-value</th>
<th>Nest Shrub Mean (S.E.)</th>
<th>Non-nest Shrub Mean (S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Shrbht (cm)</td>
<td>8.71</td>
<td>1</td>
<td>0.003</td>
<td>83.3 (6.3)</td>
<td>76.0 (5.3)</td>
</tr>
<tr>
<td>Shrbwd (cm)</td>
<td>10.64</td>
<td>1</td>
<td>0.001</td>
<td>76.6 (6.8)</td>
<td>82.6 (7.4)</td>
</tr>
<tr>
<td>ConcealS (%)</td>
<td>15.4</td>
<td>1</td>
<td>0.001</td>
<td>66.8 (5.1)</td>
<td>52.2 (6.5)</td>
</tr>
<tr>
<td>Other Sites</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ConcealO (%)</td>
<td>26.30</td>
<td>1</td>
<td>0.001</td>
<td>64.0 (2.5)</td>
<td>33.8 (2.1)</td>
</tr>
<tr>
<td>ConcealN (%)</td>
<td>4.32</td>
<td>1</td>
<td>0.04</td>
<td>67.3 (2.7)</td>
<td>48.0 (2.7)</td>
</tr>
<tr>
<td>ConcealS (%)</td>
<td>15.91</td>
<td>1</td>
<td>0.001</td>
<td>71.5 (2.5)</td>
<td>41.3 (2.5)</td>
</tr>
</tbody>
</table>

**Table 4.4.** Significant shrub-level predictors of Brewer's Sparrow nest success as determined by logistic regression.

<table>
<thead>
<tr>
<th></th>
<th>Wald $X^2$</th>
<th>df</th>
<th>P-value</th>
<th>Successful Shrub Mean (S.E.)</th>
<th>Depredated Shrub Mean (S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SC</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dstcntr (cm)</td>
<td>4.00</td>
<td>1</td>
<td>0.05</td>
<td>8.2 (2.0)</td>
<td>10.7 (1.8)</td>
</tr>
<tr>
<td>Aspect *</td>
<td>4.46</td>
<td>1</td>
<td>0.04</td>
<td>0.6 (0.1)</td>
<td>1.0 (0.1)</td>
</tr>
<tr>
<td>ConcealE (%)</td>
<td>3.91</td>
<td>1</td>
<td>0.05</td>
<td>78.3 (5.5)</td>
<td>55.7 (9.5)</td>
</tr>
<tr>
<td>Other Sites</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ConcealO (%)</td>
<td>4.87</td>
<td>1</td>
<td>0.03</td>
<td>57.7 (3.6)</td>
<td>70.7 (3.3)</td>
</tr>
<tr>
<td>ConcealN (%)</td>
<td>7.65</td>
<td>1</td>
<td>0.006</td>
<td>71.6 (3.3)</td>
<td>62.8 (4.2)</td>
</tr>
<tr>
<td>ConcealW (%)</td>
<td>6.09</td>
<td>1</td>
<td>0.01</td>
<td>53.3 (4.1)</td>
<td>65.6 (3.5)</td>
</tr>
<tr>
<td>Nstht (cm)</td>
<td>4.12</td>
<td>1</td>
<td>0.04</td>
<td>34.9 (1.9)</td>
<td>29.8 (1.8)</td>
</tr>
</tbody>
</table>

*transformed to linear scale: 0 = SW, 2 = NE*
Nest Patch

Many habitat variables were different between years in nest patches (BigSage, Bare, HrbHt, Forb) and in non-nest patches (Litter, Bare, Other) at KP. Similarly, at WL several variables differed between years in nest patches (Crust, Rabbit, Litter, Other) and non-nest patches (Crust, Rabbit, SmShrub, Other). Because so many variables differed between years, Year was added as a variable in patch-level logistic regression models.

All ground cover variables were significantly different between sites for both nest and non-nest patches; however, there was no distinct pattern that could group sites. Shrub-layer variables also differed significantly between the sites; however, SC was distinctly different than other sites. SC nest patches had the lowest coverage of BigSage, 3-TipSage and Other and the highest percentage of Rye. KP had the greatest percentage of Snow and IG had the lowest. The same pattern was shown at non-nest patches, however, Rabbit was also lowest at SC. Because the shrub cover at SC was distinctly different from the other sites, patch-level logistic regression models were developed separately for SC and the other sites were grouped together. However, because ground cover variables differed between all sites, Site was added as a variable in the logistic regression models for the three combined sites.

There were no habitat variables that could distinguish nest from non-nest patches at SC when shrub species were added separately. However, with total shrub cover in the model, nest patches were distinguished from non-nest patches by greater cover of small shrubs (Table 4.5). There was a trend toward higher TotalShrub cover at nest versus non-nest patches, although the comparison was not significant ($P = 0.08$). At the other sites, the model with separate shrub species was a better fit to the data than the one with
all shrub species combined ($AIC_c = 323.02$ vs. $339.52$). Nest patches were distinguished from non-nest patches by having more coverage of BigSage and Other, less Litter, and higher Hrbht (Table 4.5).

Table 4.5. Significant patch-level predictors of Brewer's Sparrow nest-site selection as determined by logistic regression.

<table>
<thead>
<tr>
<th></th>
<th>Wald $X^2$</th>
<th>df</th>
<th>$P$-value</th>
<th>Nest Patch Mean (S.E.)</th>
<th>Non-nest Patch Mean (S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SC SmShrub (%)</td>
<td>6.96</td>
<td>1</td>
<td>0.008</td>
<td>6.17 (1.3)</td>
<td>4.38 (0.7)</td>
</tr>
<tr>
<td>BigSage (%)</td>
<td>14.83</td>
<td>1</td>
<td>0.001</td>
<td>24.57 (1.1)</td>
<td>20.61 (1.1)</td>
</tr>
<tr>
<td>Other (%)</td>
<td>3.74</td>
<td>1</td>
<td>0.05</td>
<td>2.79 (0.6)</td>
<td>1.71 (0.3)</td>
</tr>
<tr>
<td>Litter (%)</td>
<td>7.25</td>
<td>1</td>
<td>0.007</td>
<td>12.71 (0.5)</td>
<td>13.83 (0.4)</td>
</tr>
<tr>
<td>Hrbht (cm)</td>
<td>8.61</td>
<td>1</td>
<td>0.003</td>
<td>32.83 (1.1)</td>
<td>30.00 (0.9)</td>
</tr>
</tbody>
</table>

The model for SC successful versus depredated nests that included separate shrub species, was a better fit than for all species combined ($AIC_c = 33.21$ vs. 39.58).

Successful patches had a greater percentage of Crust, but less BigSage and Other than did depredated ones, despite greater shrub cover being preferred (Table 4.6). The successful versus depredated model for the other sites with separate shrub species included was again a better fit than the model with total shrub cover ($AIC_c = 168.38$ vs. 170.82).

Successful nest patches had less Snow than depredated ones, and Site was also a significant factor (Table 4.6). They also had less grass and more bare ground than depredated nest, but the comparisons were not significant ($P = 0.08$).

These results demonstrate that many variables involved in nest site selection were unrelated to nest success. For example, the percentage of Big Sage cover at the
combined sites, a highly preferred variable, was virtually identical in successful patches and depredated ones; (24.7% successful; 24.4% depredated). High herbaceous growth was also preferred, yet heights barely differed between successful and depredated patches (33.7 cm successful; 32.0 cm depredated).

Table 4.6. Significant patch-level predictors of Brewer's Sparrow nest success as determined by logistic regression.

<table>
<thead>
<tr>
<th></th>
<th>Wald $X^2$</th>
<th>df</th>
<th>P-value</th>
<th>Successful Patch Mean (S.E.)</th>
<th>Depredated Patch Mean (S.E.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SC</td>
<td></td>
<td></td>
<td></td>
<td>N = 15</td>
<td>N = 15</td>
</tr>
<tr>
<td>Crust (%)</td>
<td>4.85</td>
<td>1</td>
<td>0.03</td>
<td>0.58 (0.3)</td>
<td>2.00 (0.5)</td>
</tr>
<tr>
<td>BigSage (%)</td>
<td>4.67</td>
<td>1</td>
<td>0.03</td>
<td>1.92 (1.4)</td>
<td>7.75 (3.2)</td>
</tr>
<tr>
<td>Other (%)</td>
<td>3.51</td>
<td>1</td>
<td>0.05</td>
<td>1.08 (0.6)</td>
<td>5.00 (2.3)</td>
</tr>
<tr>
<td>Other Sites</td>
<td></td>
<td></td>
<td></td>
<td>N = 65</td>
<td>N = 65</td>
</tr>
<tr>
<td>Snow (%)</td>
<td>6.61</td>
<td>1</td>
<td>0.01</td>
<td>1.44 (0.7)</td>
<td>3.40 (1.0)</td>
</tr>
<tr>
<td>Site</td>
<td>5.02</td>
<td>1</td>
<td>0.03</td>
<td>n/a</td>
<td>n/a</td>
</tr>
</tbody>
</table>

Because Site was a significant predictor of success at the patch level, models were re-run for the individual sites. The individual site models again showed that preferred variables associated with concealment were not always associated with success. At WL, patches with successful nests had less TotalShrub, Rock, and Forb and more Litter and Crust than did ones with depredated nests. At KP, patches with successful nests had less Snow and Grass cover, but more Other cover than ones with depredated nests. Patches with successful nests at IG had more Smshrub and Litter, but less Other than did ones with depredated nests.
All logistic regression models effectively discriminated between nest and non-nest shrubs and patches and successful and depredated shrubs and patches based on Hosmer and Lemeshow goodness-of-fit statistics (Table 4.7).

Table 4.7. Hosmer-Lemeshow goodness-of-fit tests for logistic regression models comparing nest shrubs and patches to non-nest shrubs and patches and successful to depredated nest shrubs and patches.

<table>
<thead>
<tr>
<th>Model</th>
<th>DF</th>
<th>$X^2$</th>
<th>$P &gt; X^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shrub</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC nest vs. non-nest</td>
<td>8</td>
<td>6.41</td>
<td>0.60</td>
</tr>
<tr>
<td>Other Sites nest vs. non-nest</td>
<td>8</td>
<td>1.51</td>
<td>0.99</td>
</tr>
<tr>
<td>SC successful vs. depredated</td>
<td>8</td>
<td>4.04</td>
<td>0.85</td>
</tr>
<tr>
<td>Other Sites successful vs. depredated</td>
<td>8</td>
<td>8.36</td>
<td>0.40</td>
</tr>
<tr>
<td>Patch</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SC nest vs. non-nest</td>
<td>8</td>
<td>2.79</td>
<td>0.95</td>
</tr>
<tr>
<td>Other Sites nest vs. non-nest</td>
<td>8</td>
<td>3.60</td>
<td>0.89</td>
</tr>
<tr>
<td>SC successful vs. depredated</td>
<td>8</td>
<td>2.31</td>
<td>0.88</td>
</tr>
<tr>
<td>Other Sites successful vs. depredated</td>
<td>8</td>
<td>11.14</td>
<td>0.19</td>
</tr>
</tbody>
</table>

DISCUSSION

Nest predation is the factor that most limits productivity of open-cup nesting birds. The nest concealment hypothesis suggests that this should lead to the preference for nest-site characteristics that reduce the risk of nest failure by concealing nests from potential predators (Martin 1995, Martin 1998, Clark and Shutler 1999). Brewer's Sparrows in this study preferred certain nest shrub and nest patch characteristics. Most preferred shrub variables led to better nest concealment, although this pattern varied somewhat between SC and the other sites. Taller, thinner nest shrubs selected at SC provided better concealment of nests from the south. Nest shrubs at the other sites had
more concealment from overhead and on two sides. These results suggest that Brewer's Sparrows selected nesting habitat that obscured the nest from visual detection by predators. Welstead (2002) showed that corvids, which are visual predators, are important nest predators of artificial shrub nests at nearby sites in this region. Petersen and Best (1985) found that Brewer's Sparrows in Idaho avoided both large and small sagebrush shrubs for nesting and preferred those 50-90 cm tall. Larger, older shrubs have more dead branches, open spaces and less vigorous foliage than smaller ones, and hence, offer less concealment.

The concealment hypothesis was further supported by the selection of nest patches with greater shrub cover than was available. Cover of small shrubs was greater at SC and although total shrub cover was also greater, the difference was not significant ($P = 0.08$). Brewer's Sparrows at the other three sites selected nest patches with greater coverage of big sage and other shrubs and also taller herbaceous plant growth. Greater shrub cover in nest patches may allow concealment of movements of adult birds to and from nests as well as providing many more potential nest sites for predators to search (Bowman and Harris 1980, Martin 1993). Petersen and Best (1985) found Brewer's Sparrows nesting in patches that were denser than generally available. Many other studies have found passerines to nest in patches with greater shrub cover, supporting the nest concealment hypothesis (e.g., Petit et al. 1988, Norment 1993, Misenhelter and Rotenberry 2000, Rickets and Ritchison 2000, Liebezeit and George 2002, Easton and Martin 2002).

If nest-site preferences are adaptive, then those vegetation characteristics selected should also be related to nest success. There was some support for this hypothesis; for
example, successful nests were closer to the centre of shrubs and more concealed from
the east at SC. However, at the other sites, while concealment from the north was greater
for successful nests, it was greater on the west and overhead for depredated ones.
Successful nests at the other sites were placed higher in shrubs, perhaps reducing nest
losses to ground predators. Birds may have to trade off the risk of predation of eggs or
chicks with the predation risk to adults on nests. White-tailed Ptarmigan (*Lagopus
leucurus*) nests that were more concealed were less likely to be depredated but were more
risky for incubating females (Wiebe and Martin 1998). Götmark *et al.* (1995) found that
although more concealed artificial Song Thrush (*Turdus philomelos*) nests were less
likely to be depredated, real nests were placed where concealment was intermediate.
They suggest that this supports the idea that breeding birds make trade-offs between nest
concealment for protection of young and the benefits to adults of having a view of nest
surroundings. This type of trade-off may be responsible for the inconsistent relationship
between cover at the nest and success observed in this study.

Concealment at the patch level was not associated with nest success. At SC, there
was less cover of big sage and other shrub species at successful than at depredated nests,
despite greater shrub cover being preferred. Shrub cover at SC was very patchily
distributed across the landscape as a result of the fire that left isolated patches of
sagebrush unburned and patchy shrub re-growth in wetter areas. A predator searching for
nests of shrub-nesting birds such as Brewer's Sparrows, would therefore be able to
efficiently cue into these distinct patches of shrubby vegetation in a sea of lower growing
grass and forbs. At the other sites where shrub cover was more uniform, nest searching
would be much less efficient. In the case of SC, the habitat alteration caused by the fire
resulted in shrubby patches becoming ecological traps for Brewer's Sparrows, as nests in shrubbier patches were more likely to be depredated. While they preferred to nest in patches with greater shrub cover to conceal nests, at a larger scale, these patches of shrubs were conspicuous to predators. Despite this, overall nest predation rates at SC were not higher than other sites as many nests placed in smaller shrubs in less dense patches (see Chapter 2). Because not all nests were used for habitat analysis, many of these were not sampled. A similar ecological trap scenario was observed in Dusky Flycatchers (*Empidonax oberholseri*) that selected patches of denser deciduous vegetation within forests altered by thinning, despite higher predation rates there (Easton and Martin 1999 and 2002). At the other sites, despite selection of nest patches with greater shrub and herbaceous cover, successful nest sites did not provide more concealment. In fact, snowberry cover was lower at successful nests at the other sites. Big sage cover and herbaceous height were virtually identical at successful and depredated nests suggesting that factors unrelated to nest concealment at the patch level are responsible for increased predation.

Ground cover variables associated with successful nests included less cryptogamic crust at SC and less grass but more bare ground at the other sites, although the comparisons from the other sites were not significant. While Brewer's Sparrows did not select nest sites associated with these variables, their association with nest success suggests that factors other than concealment that influence ground predator behaviour may be important. For example, if snakes and small mammals avoid crossing bare ground because of the increased predation risk, then Brewer's Sparrow nest patches with more bare ground and less grass may be less likely to experience this type of predation.
Welstead (2002) showed that small mammals were the predominant predators of artificial nests at high-density Brewer's Sparrow sites. Similarly, Vander Haegen et al. (2002) found that artificial nests in shrubsteppe habitats were more often depredated by small mammals in intact, continuous areas, but by corvids where habitat was fragmented.

Several other studies have shown that habitat variables selected by birds differ from those related to nesting success. Chase (2002) found that although Song Sparrows selected nesting habitat based on six vegetation variables, only two of those were associated with nest success and, as in this study, the relationship differed between sites. Dusky Flycatchers nested in larger shrub patches with greater shrub cover than non-nest patches, but successful nests were surrounded by fewer seedlings and saplings than were depredated ones (Liebezeit and George 2002). Ricketts and Ritchison (2000) found that vegetation variables selected by Yellow-breasted Chats did not lead to greater nesting success. Hen Harriers (Circus cyaneus) selected nesting habitat with larger heather and closer to streams than was available, but nesting success was not related to these factors (Redpath et al. 1998). Of four vegetation characteristics that distinguished Red-eyed Vireo (Vireo olivaceous) nest sites from non-nest ones, only one was related to nest success (Siepielski et al. 2001). Blackbirds (Turdus merula) selected nest sites with more cover than non-nest ones, but successful sites did not differ from depredated ones in cover density (Hatchwell et al. 1996).

The similar disconnection between habitat selection and nesting success found in the above studies and in this one may be accounted for in several ways. First, and most likely, nest-site selection and factors influencing predation risk may be operating at different spatial scales. The fact that nests on southwest-facing slopes were more...
successful than those on north-facing ones suggests an unequal distribution of predators across the landscape. While habitat characteristics selected by birds in both areas may be the same, the differential predation risk means that in one area, they may be adaptive, but in another, due to differences in predator density or composition, they may not be. It is also possible that warmer southwest facing slopes have thermal characteristics that interact with predation to improve nesting success. Welstead (2002) found that sites with higher densities of avian predators had lower densities of Brewer's Sparrows suggesting that habitat selection based on predation risk may take place at larger geographic scales than the nest-site. Misenhelter and Rotenberry (2002) found that those vegetation characteristics preferred by Sage Sparrows (Amphispiza belli) were closely associated with depredated, not successful nests. They suggest that this decoupling of habitat attractiveness and suitability led to an ecological trap for Sage Sparrows due to altered predator abundance caused by landscape-level habitat changes. Brewer’s Sparrows nest in semi-colonial aggregations, suggesting that larger-scale cues, not just local vegetation characteristics influence nest-site selection (Rotenberry et al. 1999).

Another reason for the mismatch between habitat selection and nesting success is that predators with different search strategies may lead to contradictory selection pressures, limiting optimal nest-site selection. A study of predation of artificial nests showed that while nest visibility was a major influence on predation risk, the relative importance of concealment varied with the type of predator and their nest-searching behaviour (Rangen et al. 1999). Liebeziet and George (2002) found that Dusky Flycatcher nests depredated by birds were less concealed than those depredated by mammals. Welstead (2002) demonstrated that both corvids and small mammals were
common predators of artificial nests made to resemble Brewer's Sparrow nests in this area. A garter snake was observed to depredate a nest of Brewer's Sparrow chicks during this study and snakes of several species were common at the study sites. The unpredictability of predation pressure in space and time as a result of changing populations of a diverse suite of predators may result in the disassociation between habitat attractiveness and suitability. In this study, the predation rate varied spatially and temporally between sites; it was highest at KP in 1997 and 1998 and highest at WL in 1999 and 2000 (see chapter 2). Unpredictable predation pressure could make it impossible for one set of nest site characteristics to protect nests from predation consistently. This is particularly true if predation is incidental i.e. the predator comes upon a nest while searching for other types of prey. Predation of grassland bird nests in Maine was not associated with vegetation characteristics, likely as a result of incidental predation by striped skunks (*Mephitis mephitis*; Vickery *et al.* 1992). Predation rates of artificial Sage Grouse (*Centrarcus urophasianus*) nests were higher in undisturbed than in disturbed sagebrush grasslands, likely as a result of higher lagomorph populations serving to increase the prey base for an increased density of predators such as badgers and coyotes (Ritchie *et al.* 1994).

My results suggest several recommendations for the management of Brewer's Sparrow nesting habitat. First, Brewer's Sparrows select nest shrubs greater than 76 cm in height with density of foliage cover in the range of 65% overhead and lateral cover of 65-70%. Shrub density at the 5-m patch level should average 34-50% with at least 25% big sage cover to provide enough cover for nest patches.
These recommendations will provide for habitat quality sufficient for Brewer's Sparrows to nest in. To manage for high nesting success, however, we need a better understanding of:

1. the relative amounts of predation by different predators,
2. the factors that influence the density and diversity of predators and
3. the scale at which these factors operate.

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Chapter 5:
Conclusions

Peripheral Populations

I found that annual variation in productivity in this northern peripheral population of Brewer's Sparrows was related to weather conditions. At higher elevation sites, birds traded off the benefits of early breeding in terms of the ability to re-nest, with the costs associated with an early spring storm during which many first nests were destroyed. At the low elevation site, productivity was highest when breeding began early, allowing for multiple nesting attempts before conditions became hot and dry. The differential productivity in relation to elevation suggests that productivity of Brewer's Sparrows at the northern edge of their range may be limited by environmental conditions such as spring temperature. The difference of three weeks in onset of breeding between the warm spring of 1998 and the cool spring of 1999 also suggests that spring temperature is a limiting factor. Despite large areas of sagebrush grassland habitat north of the study area, Brewer's Sparrow breeding is restricted to the extreme southern portion of the interior of B.C. This provides further support for temperature limitation at the northern edge of the range, although the timberline subspecies breeds in much cooler areas.

Recent evidence has shown that for many species, declines are occurring more rapidly in the core than at the range edges and in many cases, peripheral populations remain while those in the core decline to extinction (Channell and Lomolino 2000, Rodriguez 2002). Brewer's Sparrows, which are declining range-wide, seem to be
following this pattern since declines are steepest in core areas and less steep in some northern and southern peripheral areas.

While much can be learned about the patterns of decline across a species range by examining trends over time, only intensive studies of population dynamics throughout the range can elucidate the mechanisms that drive those patterns. This study is the first to explicitly examine demographic variation and its relation to the population viability of Brewer's Sparrows anywhere in its range. Demographic traits of populations across the range are naturally variable as a result of different resource levels and environmental conditions (Sexton et al. 1992, Blem and Blem 1995, Newton 1998). However, few studies have linked these divergent demographic characteristics to variable rates of decline across the range. One such study examined productivity in a declining population of Sage Grouse (*Centrocercus urophasianus*) at the northern edge of the range in southern Alberta (Aldridge and Brigham 2001). This study showed that while breeding success was within the range observed for populations further to the south, chick survival to 50 days was only half the level needed for a stable population, and thus, was likely the cause of regional population decline. Breininger (1999) showed how different rates of natal dispersal throughout the range of a declining Florida Scrub-Jay population were related to rates of population decline. Steeper declines in peripheral areas resulted from recruitment of young from peripheral areas into territories left vacant in the range core.

My assessment of Brewer's Sparrow population viability suggests that the British Columbia population would go rapidly extinct without immigration from further south. This is consistent with work by Curnutt et al. (1996) who showed that peripheral
populations of nine species of grassland sparrows were more variable over time and less abundant than core populations. They suggested that populations at the edges of the ranges were maintained by immigration from range cores. My population model also demonstrated that variation in adult survival had the most influence on the population trajectory and that increasing the frequency of low survival years led to steeper declines. Sufficient fat reserves must be obtained in non-breeding areas for birds to withstand the rigours of migration and arrive in good condition to breed. Birds in northern peripheral populations, which have the furthest to travel, may be at a disadvantage, especially in years of poor conditions in non-breeding areas. Over-winter survival rates from 1998-1999 were only half the level of the other two years of the study. The dry conditions during that La Niña winter may have prevented wintering Brewer's Sparrows from obtaining enough food to survive the winter or made them less able to survive migration.

In this study, I characterized the demographic attributes of this population and built a stochastic demographic viability model to generate hypotheses about how those characteristics affected the population trend. Population-specific demographic rates must be examined in relation to habitat characteristics in other portions of the breeding range to determine the mechanisms driving the range-wide decline. This work is currently underway and should lead to a better understanding of population processes in core versus peripheral populations (P. Krannitz, pers. comm.).

Conservation and Management of Brewer's Sparrows in British Columbia

Brewer’s Sparrows are provincially red-listed (endangered) in British Columbia, due to their restricted range and threatened shrubsteppe habitat. In this region, they breed
in relatively large tracts of sagebrush grassland and are at highest densities where there is a healthy understory of perennial forbs such as Lupine and Parsnip-flowered Buckwheat (Paczek 2002). Sites with high densities of Brewer's Sparrows have more forbs and associated arthropods than low density ones, providing important prey resources during the breeding season (Krannitz unpublished). Much of the shrubsteppe habitat in southern British Columbia has been removed by intensive agriculture and urbanization. Areas remaining are highly fragmented and habitat quality has been affected by intensive livestock grazing. Grazing cattle can break branches from sagebrush shrubs, thereby reducing their quality as nesting substrate, and alter the understory layer by removing native grasses and forbs and increasing the density of exotic, invasive weeds, decreasing important foraging habitat (West 1996). My population model suggested that under the best-case scenario when adult survival was relatively high, productivity was an important factor in driving the population trend. I recommend reducing stocking rates and increasing grazing rotation times to mitigate the impacts of livestock. This would help to maintain high quality breeding habitat in this region. An experimental approach to examining the effects of these mitigation methods on conservation lands such as the White Lake Biodiversity Ranch and the South Okanagan Grasslands Park should be taken in order to develop a set of best management practices that can be applied to crown leases and licenses and private ranch lands.

Reports from early European explorers in the Great Basin region indicate that much of the landscape was dominated by shrubs, with grass-dominated areas restricted to wet valley bottoms and hillsides (Vale 1975). Wildfires and those set by First Nations people were important in structuring the vegetation communities in this region before
European settlement. The fire cycle at that time has been estimated to be from 20-25 years (Wright and Bailey 1982). This would have resulted in a patchy distribution of sagebrush habitats in different stages of recovery from fire, a situation to which Brewer's Sparrows would have been adapted. This may account for the semi-colonial nature of this species, which occurs in high densities in patches of high quality habitat (Rotenberry et al. 1999).

In combination with livestock grazing, fire suppression in recent decades has altered the vegetation community in combination with livestock grazing to result in denser sagebrush cover, less understory vegetation and forest encroachment (Tisdale and Hironaka 1981, West 1988, Turner and Krannitz 2001). This may result in lower abundance and quality of breeding habitat for Brewer's Sparrows, which require medium density of mid-sized sagebrush shrubs. However, in some areas outside of B.C., the invasion of the exotic Cheatgrass (Bromus tectorum) has dramatically increased fire cycles (Knick and Rotenberry 1997). Cheatgrass dries out in late May or early June and grows in dense mats, unlike the scattered distribution of native bunchgrasses, and is, therefore, more prone to hotter, more widespread fires. After several fires, the resulting plant community is dominated by Cheatgrass and the shrub layer disappears. One of my study sites, SC, was burned in a wildfire in 1994 and lightly grazed by horses. When I began work in 1997, there were a few remnant patches of Big Sagebrush, in which Brewer's Sparrows nested in high density. Most of the site was covered in forbs and grasses, with scattered Common Snowberry patches in wetter draws. I found Brewer's Sparrows to nest in a much wider variety of plant species at SC than at the other three sites including: Rose sp., Common Rabbitbrush, Giant Wildrye, Silky Lupine,
Lemonweed, Diffuse Knapweed, Bluebunch Wheatgrass, Tarragon, Arrow-leaved Balsamroot and Mustard sp. This result demonstrated that, although they prefer Big Sagebrush, they are plastic in their nest substrate choices when sagebrush is not available, likely a result of being adapted to fire-prone ecosystems with a heterogeneous cover of sagebrush across the landscape. Despite the wide variety of nest substrates, productivity at SC was not consistently low, in fact, it was highest at this site in 2000. Overall, nest predation rates were lower at SC than at the other sites, suggesting that fire may lower predator numbers, such as snakes and small mammals (W. Klenner, pers. comm.), although a study with replicated burned and non-burned plots would be needed to assess this.

The Identified Wildlife Management Strategy for Brewer's Sparrows in British Columbia recommends not allowing Brewer's Sparrow habitat to burn (MWLAP, B.C. 2002). However, if habitat remains unburned for long periods of time, it may become less productive for Brewer's Sparrows. I recommend that some wildfires or prescribed burns be allowed in areas where livestock grazing is restricted and Cheatgrass invasion is not a problem, to maintain the natural heterogeneity of habitat patches across the landscape.

Nest predation was the dominant factor limiting productivity in this study. A diverse suite of predators is responsible for this predation including corvids, small mammals and snakes (Welstead 2002, Mahony pers. obs.). While all of these predator species are native to the region, human-caused habitat alterations may be responsible for changes in their abundance. According to Breeding Bird Survey data, Common Ravens (Corax corax) have increased by 2.4%/year from 1996-2000 in British Columbia and
American Crows (*Corax brachyrhynchos*) are increasing across the continent (Sauer et al. 2001). Corvid species, especially American Crows, are well adapted to human altered habitats, which may be responsible for their increases. If these population trends continue, predation pressure on Brewer's Sparrows may increase. I found that nest predation rates varied across years and sites indicating that predator dynamics likely vary over larger spatial scales than my study sites and that annual weather conditions may have differential effects on predator species. To maintain high regional productivity, I recommend that Big Sagebrush habitat be maintained at different elevations across the region to allow for this spatial and temporal variation in predation rates. This way, in any given year, high productivity at some sites can offset poor production at others and high productivity can be traded off between sites as predation pressure shifts.

My population models suggested the importance of immigration and adult survival to population viability of Brewer's Sparrows in this region. The B.C. population may be maintained by recruitment of yearling birds from other areas of the range where populations are stable, such as nearby Washington. A recent genetic study found moderate to high levels of gene flow between the Washington and B.C. populations, evidence for the importance of immigration in population dynamics in the region (Croteau 2002). While recruitment of young birds from outside B.C. may be crucial to maintaining B.C. populations, recruitment of birds produced in B.C. may contribute to populations in other regions, especially Washington. If this is the case, productivity in B.C. may have important consequences for the species at larger spatial scales. Hence, management to maintain productive breeding habitat across regions may be important, not just for local populations, but to the range-wide population trend.
The population models I developed were most sensitive to adult survival. If this is truly the case, it suggests that maintaining suitable habitat in wintering areas and migratory stop-over sites is integral to population viability. The arid shrub regions, used by Brewer's Sparrows during migration and winter, have experienced habitat alteration similar to that on the breeding grounds (i.e., increased urbanization and agriculture, including livestock grazing; Hutto 1986, Paige and Ritter 1999, Vickery et al. 1999).

The ecology of the Brewer's Sparrows in the non-breeding season is not well understood. Studies of foraging ecology and the relationship between food resources, weather conditions and habitat quality in wintering and migration habitat are needed to assess the role of habitat alteration in these areas on the declining status of this species.

When assessing conservation options suggested by demographic models, managers must not only explore which demographic rates most affect population viability, but which can be most easily affected by management activities (Beissinger and Westphal 1998, Morris and Doak 2002). My population models suggest that while adult survival may have the most influence on population trend, productivity was almost as important in the best-case model. This suggests that increasing productivity may offset reduced survival. It may be easier to increase productivity by habitat management in breeding areas where more is known about how to affect change than in non-breeding areas where we currently have little information, and where social and economic conditions may make conservation and management more difficult. We may be able to maintain populations by keeping productivity high until the necessary ecological studies can be undertaken to design habitat management options for non-breeding areas.
To my knowledge, this study is the first to examine population dynamics and population viability of Brewer's Sparrows. I showed that population dynamics are driven by factors operating at multiple spatial and temporal scales. Productivity was affected by predation rates that varied annually and spatially, likely by predator dynamics operating at regional scales. It was also affected by local storm events and possibly by global climate cycles, which affected the onset of breeding. My population viability analysis suggested that population viability was most sensitive to adult survival which varied annually but not by site. Adult survival may be tightly linked to large-scale climate cycles such as ENSO events.

Finally, the B.C. population may be maintained by immigration from other parts of the species range, meaning that the long-term prospects for this population may be tied to the range-wide population trend which is showing steady decline. Because of this multi-scale external control of population dynamics, the fortunes of the south Okanagan-Similkameen population of Brewer's Sparrows can not be managed solely by focusing conservation efforts in this small region. Wider-scale, multilateral conservation programs such as Partners in Flight can ensure that local conservation efforts are set in the context of range-wide population trends. The current emphasis of conservation programs for most migratory birds is on the breeding season. This will have to change to include all aspects of the life cycle if conservation programs are to be successful.
LITERATURE CITED


